

Informations in models of evolutionary dynamics

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Biological organisms adapt to changes by processing informations from different sources, most notably from their ancestors and from their environment. We review an approach to quantify these informations by analyzing mathematical models of evolutionary dynamics, and show how explicit results are obtained for a solvable subclass of these models. In several limits, the results coincide with those obtained in studies of information processing for communication, gambling or thermodynamics. In the most general case, however, information processing by biological populations shows unique features that motivate the analysis of specific models.

I. INTRODUCTION

Concepts from information theory are central to many quantitative studies of information processing in biology (1). In particular, the mutual information is commonly used to analyze input-output relationships in cellular processes such as biochemical sensing and transcriptional regulation (2–5). As a generic measure of information transmission, the mutual information has indeed a number of attractive mathematical properties (6). As a measure of biological information, however, it has several shortcomings: it does not account for the organization of cells into populations or for the role of inherited information and, more generally, its connection to evolutionary fitness may be questioned. How should the mutual information be amended to account for these features? Are such amendments always decreasing the value of information, thus conferring to the mutual information the role of an “ideal” upper bound? Or can these amendments have a major incidence on the way information is optimally processed by a cell?

A principled approach to these questions is to follow Shannon’s example (7) in defining and studying an abstract mathematical model that captures the essence of the problem of interest without directly (or axiomatically) prescribing a formula for quantifying information. This formula is instead expected to emerge as a property of the model. We review here such an approach to the problem of formalizing information processing in growing populations (8). Because of similarities but also differences with engineering problems, this approach leads to measures of informations that are related but not identical to those obtained from models of communication.

One crucial difference is that cells reproduce and form populations. This feature is common to problems of gambling and financial investment. The first analysis of the value of information in growing populations was in fact performed by Kelly in relation to horse-race gambling (9). He found that the mutual information emerges from the analysis of his model as it does from Shannon’s model of communication (7). His results were later extended to show that, in more general models, the mutual information provides only an upper bound on the value of information (6; 10). Several studies have pointed out the relevance of these results to biological populations (11–13). In one of them (8), we analyzed two other generic limitations of the mutual information as a measure of the value of biological information: its failure to account for constraints of causality, which has also been examined in the context of gambling (14), and its failure to account for the distributed nature of biological information processing, where each individual cell processes its own information, which has no equivalent in gambling. This second feature implies that the value of information may exceed the value given by the mutual information (8; 15).

Practically, deriving measures of information from abstract models is limited by the difficulty of analyzing mathematically models of sufficient generality. We show here how explicit formulae for the values of acquired and inherited informations in growing populations can be obtained for a class of solvable Gaussian models (16). Gaussian approximations are common in studies of information processing by biochemical networks (15; 17–19). Gaussian models of population dynamics have also their counterpart in several other fields. In information theory, they correspond to models of transmission of continuous signals in presence of additive white Gaussian noise (20). In population genetics, Gaussian models are at the foundation of quantitative genetics, which studies the evolution of continuous traits (21). In stochastic control theory, they are related to the Kalman filter, a tracking algorithm based on noisy measurements (22). In physics finally, we shall present a formal mapping to the problem of controlling by feedback a Brownian particle in a tunable harmonic potential.

A more general connection between measures of information in growing populations and in stochastic thermodynamics was presented recently by Vinkler, Permuter and Merhav (23). Quantifying the value of information for controlling thermodynamical systems has been the object of many studies (24). Most of them follow the approach

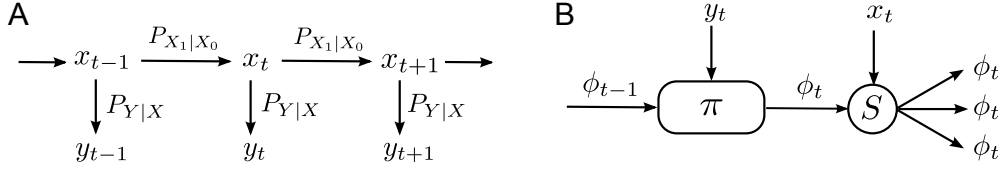


FIG. 1 Discrete model – **A**. The environment is a stochastic process with two components: a selective pressure x_t and a cue y_t . The selective pressure x_t follows a Markov process with conditional probability $P_{X_1|X_0}(x_t|x_{t-1})$ and the cue y_t derives from x_t with conditional probability $P_{Y|X}(y_t|x_t)$. **B**. A member of the population at generation t receives two informations, an inherited type ϕ_{t-1} , which may differ from individual to individual, and an environmental cue y_t , which is common to all individuals of the same generation t . From these two informations, the type ϕ_t is generated with conditional probability $\pi(\phi_t|\phi_{t-1}, y_t)$. The fitness of ϕ_t given the selective pressure x_t decides the number ξ of descendants of the individual, with $S(\phi_t, x_t)$ representing the mean value of ξ given ϕ_t and x_t . The descendants inherit the type ϕ_t of their ancestor and are themselves subject to the next environment (x_{t+1}, y_{t+1}) . At any given time, the composition of the population is characterized by the number $N_t(\phi_t)$ of individuals of each type ϕ_t .

advocated here: a model is defined based on thermodynamical principles and a measure for the value of information is inferred from an analysis of its physical properties; for instance, this value is identified with the maximal work that can be extracted based on microscopic measurements (24). Given the different premises, it is all the more interesting to find that analogous formulae emerge when analyzing information processing in evolutionary dynamics and thermodynamics.

The present work thus aims at connecting and extending different lines of work. In the first part, we review the problem of quantifying informations in a discrete model of growing population (8). Several aspects are common between this problem in gambling and in biology and we highlight the features specific to biological populations. In a second part, we show how this model becomes analytically solvable in a continuous limit. The Gaussian model thus defined extends a model studied by Haccou and Iwasa (25) and can itself be extended to a more general model (16). In a third part, we present and develop an analogy to problems of stochastic thermodynamics (23), which we apply to Gaussian models. Finally, we conclude by discussing some open challenges.

II. DISCRETE MODEL

We start by reviewing the properties of a discrete model of information processing in growing populations (8).

A. Definition

The model considers a population of non-interacting individuals reproducing asexually in an independently varying environment (Figure 1). This environment is characterized by a state x_t , whose dependency on past history $x^{t-1} = (x_1, \dots, x_{t-1})$ is represented by a conditional probability $P_{X_t|X^{t-1}}(x_t|x^{t-1})$ (we follow the convention of denoting random variables by upper-cases and values that they take by lower-cases). An individual at generation t is characterized by an internal discrete state, ϕ_t , called its “type”, which determines its reproductive success. This reproductive success is quantified by $S(\phi, x_t)$, the expected number of descendants in the following generation, given the internal state ϕ_t and the external state x_t . If $R(\xi|\phi_t, x_t)$ is the probability for an individual of type ϕ_t and in environment x_t to have ξ descendants in the next generation (including itself) this reproductive success is thus given by $S(\phi_t, x_t) = \langle \xi \rangle_{\phi_t, x_t} = \sum_{\xi} \xi R(\xi|\phi_t, x_t)$.

The type ϕ_t of an individual may depend on two things: the type ϕ_{t-1} of its parent and a cue y_t correlated to the selective pressure x_t by a conditional probability $P_{Y_t|X_t}(y_t|x_t)$, which we assume to be fixed: $P_{Y_t|X_t}(y_t|x_t) = P_{Y_1|X_1}(y_t|x_t)$ [also abbreviated $P_{Y|X}(y_t|x_t)$]. The ancestral type ϕ_{t-1} represents an inherited information and the perceived signal y_t an acquired information. The relationship between ϕ_t , ϕ_{t-1} and y_t is generally considered to be stochastic, and characterized by a conditional probability $\pi(\phi_t|\phi_{t-1}, y_t)$. This conditional probability π encodes the information processing strategy followed by each individual of a population, each having its own ϕ_{t-1} and ϕ_t but experiencing the same x_t and y_t .

While the model can be studied more generally (8), we analyze it here under two simplifying assumptions:

- (i) We assume that the environment is stationary, ergodic and Markovian, with $P_{X_t|X^{t-1}}(x_t|x^{t-1}) = P_{X_1|X_0}(x_t|x_{t-1})$.
(ii) We assume that $S(\phi_t, x_t)$ is of the form

$$S(\phi_t, x_t) = K(x_t)\Delta(x_t|\phi_t) \quad \text{with} \quad \Delta(x_t|\phi_t) \geq 0 \quad \text{and} \quad \sum_{x_t} \Delta(x_t|\phi_t) = 1. \quad (1)$$

This assumption means that no type ϕ_t has a systematic advantage when considering all possible environments x_t (25). (Here and below, a notation of the type $A(u|v)$ always signifies that A is a transition matrix, with $A(u|v) \geq 0$ and $\sum_u A(u|v) = 1$ for all v .)

B. Fitness and optimality

The dynamics of the model is summarized by a recursion for $N_t(\phi_t)$, the expected number of individuals of type ϕ_t at generation t ,

$$N_t(\phi_t) = \sum_{\phi_{t-1}} S(\phi_t, x_t) \pi(\phi_t|\phi_{t-1}, y_t) N_{t-1}(\phi_{t-1}), \quad (2)$$

where the series of environmental states $x^t = (x_1, \dots, x_t)$ and cues $y^t = (y_1, \dots, y_t)$ are considered as externally fixed.

Quantifying the values of the inherited information ϕ_{t-1} and acquired information y_t requires a well-defined fitness function. This fitness function should indicate the outcome of natural selection when two populations with different strategies π_1 and π_2 , defining two “species”, are competing. As this outcome may be stochastic, such a fitness function need not exist (or may depend on the particular realization of the stochastic processes). For our simple model, however, a population will, in the long term, either become extinct or grow exponentially. In the second case, the rate of exponential growth, Λ , depends on the strategy π , the selection S , and the environmental parameters $P_{X_1|X_0}$ and $P_{Y_1|X_1}$, but not on the particular realization of the dynamics [mathematical details may be found in (8)]. This growth rate thus defines a fitness function to compare the long-term value of different strategies π .

More precisely, the growth rate is given by the limit

$$\Lambda = \lim_{t \rightarrow \infty} \frac{1}{t} \ln \frac{N_t}{N_0}, \quad (3)$$

where $N_t = \sum_{\phi_t} N_t(\phi_t)$ represents the expected total population size at generation t . If the environment is stationary and ergodic, which we shall assume, Λ can also be written as

$$\Lambda = \mathbb{E}[\ln W_t], \quad (4)$$

where $W_t = N_t/N_{t-1}$ represents the factor by which the population size is multiplied between two successive generations, and \mathbb{E} is an expectation with respect to the external random variables X^t and Y^t .

$\Lambda(\pi)$ defines a relevant measure of fitness in the sense that, in the long run ($t \rightarrow \infty$) and all other things being equal, a population following strategy π_1 will almost surely exponentially out-number a population following π_2 if and only if $\Lambda(\pi_1) > \Lambda(\pi_2)$ (provided the population does not become extinct). An optimal strategy $\hat{\pi}$ can therefore be defined as a strategy optimizing $\Lambda(\pi)$.

C. Informations

We define the value of an information as the increment of fitness that it may confer. This involves a comparison between the growth rate of two models, one in which the information is available, and one in which it is not. Mathematically, no information can be acquired when π is of the form $\pi(\phi_t|\phi_{t-1})$ and no information is inherited when it is of the form $\pi(\phi_t|y_t)$. More generally, let \mathcal{P}_0 be a subset of the set \mathcal{P}_1 of admissible strategies in which π is prevented from accessing a particular information. Then we define the value of this information as

$$I = \max_{\pi \in \mathcal{P}_1} \Lambda(\pi) - \max_{\pi \in \mathcal{P}_0} \Lambda(\pi). \quad (5)$$

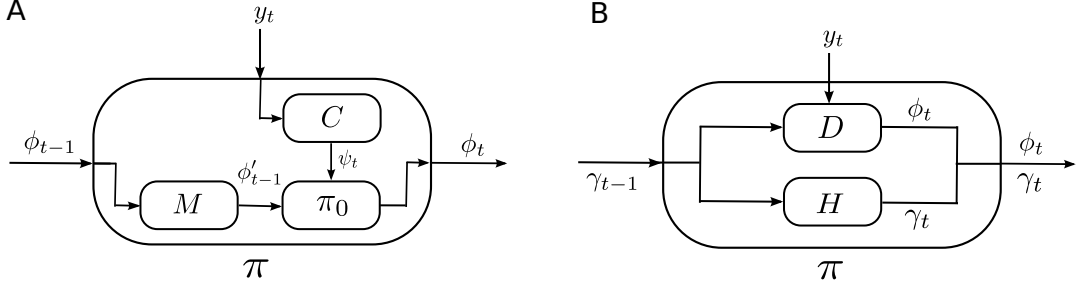


FIG. 2 Constrained information processing – The conditional probability $\pi(\phi_t|\phi_{t-1}, y_t)$ which decides the type ϕ_t of an individual given the inherited type ϕ_{t-1} and the environmental cue y_t (Figure 1) may be constrained. **A.** Replication may be subject to mutations such that the individual effectively inherits ϕ'_{t-1} with conditional probability $M(\phi'_{t-1}|\phi_{t-1})$. Sensing may be subject to noise such that the individual effectively perceives ψ_t with conditional probability $C(\psi_t|y_t)$. Given these two elements, an individual generates its type ϕ_t with conditional probability $\pi_0(\phi_t|\phi'_{t-1}, \psi_t)$. While the environmental cue y_t is common to all members of the population at a given generation t , the perceived signal ψ_t may differ from individual to individual. **B.** The type may have two components: a phenotype ϕ_t which decides the number of descendants via $S(\phi_t, x_t)$ and a genotype γ_t which defines the information transmitted to these descendants. The first may be described by a conditional probability $H(\gamma_t|\gamma_{t-1})$ and the second by $D(\phi_t|\gamma_{t-1}, y_t)$, where γ_{t-1} represent the inherited genotype, which, by definition, is the only component of the type $(\phi_{t-1}, \gamma_{t-1})$ to be inherited.

In particular, the value of acquired information I_{acquired} is defined by considering the subset \mathcal{P}_0 of strategies of the form $\pi(\phi_t|\phi_{t-1})$, and the value of inherited information $I_{\text{inherited}}$ of the form $\pi(\phi_t|y_t)$. By taking for \mathcal{P}_0 the subset of strategies of the form $\pi(\phi_t)$, we also define the joint value of the two informations, I_{tot} , which is generally *not* the sum $I_{\text{acquired}} + I_{\text{inherited}}$, since $I_{\text{tot}} = \max_{\pi(\phi_t|\phi_{t-1}, y_t)} \Lambda(\pi) - \max_{\pi(\phi_t)} \Lambda(\pi) \neq \max_{\pi(\phi_t|\phi_{t-1}, y_t)} \Lambda(\pi) - \max_{\pi(\phi_t|\phi_{t-1})} \Lambda(\pi) + \max_{\pi(\phi_t|\phi_{t-1}, y_t)} \Lambda(\pi) - \max_{\pi(\phi_t|y_t)} \Lambda(\pi)$.

Additional constraints may be present that restrain \mathcal{P}_0 and \mathcal{P}_1 to a subclass of admissible strategies. For instance, the transmission of inherited information may be noisy because of random mutations following replication, with π necessarily of the form $\pi(\phi_t|\phi_{t-1}, y_{t-1}) = \sum_{\phi'_{t-1}} \pi_0(\phi_t|\phi'_{t-1}, y_t) M(\phi'_{t-1}|\phi_{t-1})$, where $M(\phi'_{t-1}|\phi_{t-1})$ is a given mutational matrix, and where only the conditional probability $\pi_0(\phi_t|\phi'_{t-1}, y_t)$ is subject to optimization (Figure 2A). This corresponds to replacing Eq. (2) by $N_t(\phi_t) = \sum_{\phi'_{t-1}} S(\phi_t, x_t) \pi_0(\phi_t|\phi'_{t-1}, y_t) N'_{t-1}(\phi'_{t-1})$ where $N'_{t-1}(\phi'_{t-1}) = \sum_{\phi_{t-1}} M(\phi'_{t-1}|\phi_{t-1}) N_{t-1}(\phi_{t-1})$ represents the number of individuals mutated to ϕ'_{t-1} .

Similarly, the acquisition of an information from the environmental variable y_t may be limited by a noisy sensor $C(\psi_t|y_t)$, with π constrained to be of the form $\pi(\phi_t|\phi_{t-1}, y_t) = \sum_{\psi_t} \pi_0(\phi_t|\phi_{t-1}, \psi_t) C(\psi_t|y_t)$ (Figure 2A). This constraints introduces a distinction between two types of informations: y_t , which is a feature of the environment and is common to all members of the population at generation t , and ψ_t , which is associated with a particular individual (we use Roman letters for environmental variables and Greek letters for individual variables). For instance, y_t may represent the concentration of one of several constituents of the environment, related to x_t by $P_{Y|X}(y_t|x_t)$, and ψ_t the concentration of this constituent as perceived by a particular individual, given its noisy sensor $C(\psi_t|y_t)$. The cue y_t and the sensor C are common to all individuals but not necessarily the perceived signal ψ_t . This decomposition may be viewed as the counterpart at a population level of the decomposition between extrinsic and intrinsic noise at the individual level (26): as intrinsic noise corresponds to intra-individual variations and extrinsic noise to inter-individual variations in gene expression, the intrinsic information ψ_t corresponds to intra-generation variations and the extrinsic information y_t to inter-generation variations in information sensing. This distinction becomes important when evaluating the value of the information provided by the sensor $C(\psi_t|y_t)$, as opposed to the value of the information provided by the “environmental channel” $P_{X|Y}(y_t|x_t)$ (see examples below).

Another biologically motivated constraint on π is the decomposition of the type of an individual into a genotype, which is inherited and transmitted, and a phenotype on which selection acts. A generic model making this distinction is for instance defined by the recursion

$$N_t(\gamma_t) = \sum_{\phi_t, \gamma_{t-1}} S(\phi_t, x_t) H(\gamma_t|\gamma_{t-1}, \phi_t, z_t) D(\phi_t|\gamma_{t-1}, y_t) N_{t-1}(\gamma_{t-1}), \quad (6)$$

where $D(\phi_t|\gamma_{t-1}, y_t)$ specifies how the phenotype ϕ_t stochastically depends on the inherited genotype γ_{t-1} and some aspect y_t of the environment and $H(\gamma_t|\gamma_{t-1}, \phi_t, z_t)$ how the transmitted genotype γ_t depends on the inherited genotype

and some possibly different aspect z_t of the environment (Figure 2B). As shown in Appendix A, this model corresponds to Eq. (2) when π is constrained to a particular set of admissible strategies. The model defined by Eq. (6), however, has two acquired informations: y_t at the phenotypic level and z_t at the genotypic level (which each may be decomposed into extrinsic and intrinsic contributions). This extension corresponds to a discrete version of the model proposed in (16) and illustrates the fact that multiple acquired informations may be defined and quantified. Similarly, the model can be extended to deal with multiple inherited informations, for instance to represent a genetic and an epigenetic contribution to heredity.

D. Solvable limits

In two limits, Eq. (2) factorizes into a recursion that involves only the total population size $N_t = \sum_{\phi_t} N_t(\phi_t)$. The first limit is when the environment is maximally selective, so that only one type ϕ_t , which may be defined without loss of generality as $\phi_t = x_t$, can survive in each environmental state x_t ,

$$S(\phi_t, x_t) = K(x_t)\delta(x_t, \phi_t) \quad [\text{perfect selectivity}] \quad (7)$$

where $K(x_t)$ represents the multiplicative rate of the surviving type, and δ denotes the Kronecker symbol, with $\delta(x_t, \phi_t) = 1$ if $\phi_t = x_t$ and 0 otherwise. This corresponds to $\Delta(x_t|\phi_t) = \delta(x_t, \phi_t)$ in Eq. (1). In this case, $N_t = N_t(x_t)$ and

$$N_t = W_t N_{t-1} \quad \text{with} \quad W_t = K(x_t)\pi(x_t|x_{t-1}, y_t). \quad (8)$$

The second limit is in absence of inheritance, when the current type ϕ_t of an individual cannot depend on its ancestral type ϕ_{t-1} ,

$$\pi(\phi_t|\phi_{t-1}, y_t) = \pi(\phi_t|y_t) \quad [\text{no inheritance}] \quad (9)$$

which implies

$$N_t = W_t N_{t-1} \quad \text{with} \quad W_t = \sum_{\phi_t} S(\phi_t, x_t)\pi(\phi_t|y_t). \quad (10)$$

Given the assumption made in Eq. (1), this may be rewritten as $N_t = K(x_t)\tilde{\pi}(x_t|y_t)N_{t-1}$, as in Eq. (8), but with an effective strategy $\tilde{\pi}$ defined by

$$\tilde{\pi}(x_t|y_t) = \sum_{\phi_t} \Delta(x_t|\phi_t)\pi(\phi_t|y_t). \quad (11)$$

The effective strategy $\tilde{\pi}$ is here constrained to a particular subset \mathcal{P}_1 , as in the examples discussed above.

The conjunction of the two limits, perfect selectivity and no inheritance, defines Kelly's model (9), where

$$N_t = W_t N_{t-1} \quad \text{with} \quad W_t = K(x_t)\pi(x_t|y_t), \quad (12)$$

and therefore

$$\Lambda = \mathbb{E}[\ln W_t] = \mathbb{E}_X[\ln K(X)] + \mathbb{E}_{X,Y}[\ln \pi(X|Y)]. \quad (13)$$

where $\mathbb{E}_X \ln K(X) = \sum_x P_X(x) \ln K(x)$ with $P_X(x) = P_{X_t}(x)$ describing the probability of $x_t = x$ (since the environment is assumed to be stationary, it is independent of t), and where $\mathbb{E}_{X,Y}[\ln \pi(X|Y)] = \sum_{x,y} P_{X,Y}(x,y) \ln[\pi(x|y)]$ with $P_{X,Y}(x,y) = P_{Y|X}(y|x)P_X(x)$ describing the joint probability of $(x_t, y_t) = (x, y)$.

In the original formulation of this model (9), N_t is a capital that a gambler bets on successive horse races and x_t represents the horse winning on race t , $K(\phi_t)$ the odds for horse ϕ_t (the ratio of the full payout to the stake if it wins) and y_t a side-information hinting at the identity of x_t . The betting strategy $\pi(\phi_t|y_t)$ defines the fraction of capital bet on each horse ϕ_t given the information y_t , which the gambler wants to choose so as to maximize its cumulative gain $N_t = \prod_{k=1}^t W_k N_0$. In this interpretation, an individual corresponds to a particular unit of currency, say a 1€ coin, and the "type" of a coin to the horse on which it is bet.

The analogy extends to models with finite selectivity, corresponding to multiple horses having non-zero return and to models with inheritance, corresponding to a gambler with memory (6). Some aspects of information processing in biological population have, however, no analogy in gambling, such as the distinction between extrinsic and intrinsic informations. Information processing is indeed centralized in gambling, where a gambler controls each of its coins, while it is distributed in biology, where each member of a population can act independently and stochastically.

In the following two sections, we summarize the properties of the model in each of the two generally solvable limits of no inheritance and perfect selectivity, before introducing a continuous model that can be solved beyond these two limits. We refer to (6; 8; 14) for a derivation of the results.

E. No inheritance

Assuming no inheritance, i.e., π constrained to the form $\pi(\phi_t|y_t)$, we can write the growth rate as (see Appendix B)

$$\Lambda = \Lambda^* - H(X) + I(X; Y) - \mathbb{E}_Y[D(P_{X|Y}(\cdot|Y) \|\tilde{\pi}(\cdot|Y))], \quad (14)$$

where $\tilde{\pi}$ is the effective strategy defined in Eq. (11). In this decomposition, each term has an interpretation of its own (6):

- $\Lambda^* = \mathbb{E}_X \ln K(X) = \sum_x P_X(x) \ln K(x)$ corresponds to a maximal growth rate, possibly achievable only if knowing exactly the sequence of environmental states;
- $H(X) = -\sum_x P_X(x) \ln P_X(x)$ is the entropy of X_t , and represents here a cost due to the stochasticity of environmental process;
- $I(X; Y)$ is the mutual information between the cue Y_t and the selective variable X_t , defined by

$$I(X; Y) = \sum_{x,y} P_{Y|X}(y|x) P_X(x) \ln \frac{P_{Y|X}(y|x)}{P_Y(y)}, \quad (15)$$

where $P_Y(y) = \sum_x P_{Y|X}(y|x) P_X(x)$ is the probability of $y_t = y$. It can also be written $I(X; Y) = H(Y) - H(Y|X)$ or $I(X; Y) = H(X) - H(X|Y)$ if introducing the conditional entropy $H(Y|X) = -\sum_{x,y} P_{X,Y}(x,y) \ln P_{Y|X}(y|x)$. The mutual information represents here a gain due to the information about X_t that is contained in Y_t and is zero if and only if X_t and Y_t are independent random variables;

• $\mathbb{E}_Y[D(P_{X|Y}(\cdot|Y) \|\tilde{\pi}(\cdot|Y))] = \sum_y P_Y(y) D(P_{X|Y}(\cdot|y) \|\tilde{\pi}(\cdot|y))$ represents the cost of following a suboptimal strategy. It involves a relative entropy, which is generally defined between two distributions $P(x)$ and $Q(x)$ as

$$D(P\|Q) = \sum_x P(x) \ln \frac{P(x)}{Q(x)}. \quad (16)$$

$D(P\|Q) \geq 0$ and $D(P\|Q) = 0$ if and only if $P = Q$. It also involves $P_{X|Y}$, the conditional probability of X_t given Y_t , which by Bayes' rule is given by

$$P_{X|Y}(x|y) = \frac{P_{Y|X}(y|x) P_X(x)}{P_Y(y)}. \quad (17)$$

Since π appears only in the last term of Eq. (14), which is necessarily non-negative, the optimal growth rate is

$$\hat{\Lambda} = \Lambda^* - H(X) + I(X; Y) - \min_{\pi} \mathbb{E}_Y[D(P_{X|Y}(\cdot|Y) \|\tilde{\pi}(\cdot|Y))]. \quad (18)$$

In computing the minimum, two situations may arise. If the equation $\tilde{\pi} = P_{X|Y}$ has a solution in π , then this solution optimizes the growth rate by reducing to zero the relative entropy term, and $\hat{\Lambda} = \Lambda^* - H(X) + I(X; Y)$. Otherwise, $\hat{\Lambda} < \Lambda^* - H(X) + I(X; Y)$.

When considering the value of acquired information, the optimal growth rate in absence of information, $\hat{\Lambda} = \Lambda^* - H(X) - \min_{\pi} D(P_X \|\tilde{\pi})$, must also be evaluated [minimum over \mathcal{P}_0 in Eq. (5)]:

$$I_{\text{acquired}} = I(X; Y) - \min_{\pi} \mathbb{E}_Y[D(P_{X|Y}(\cdot|Y) \|\tilde{\pi}(\cdot|Y))] + \min_{\pi} D(P_X \|\tilde{\pi}). \quad (19)$$

Since $\tilde{\pi} = P_X$ has a solution whenever $\tilde{\pi} = P_{X|Y}$ has a solution $\hat{\pi}(x|y)$ [given by $\pi(x) = \sum_y \hat{\pi}(x|y) P_Y(y)$], three cases must be considered: (i) $\tilde{\pi} = P_{X|Y}$ has a solution (implying that $\tilde{\pi} = P_X$ has one); (ii) $\tilde{\pi} = P_X$ has a solution but not

$\tilde{\pi} = P_{X|Y}$; (iii) $\tilde{\pi} = P_X$ has no solution (implying that $\tilde{\pi} = P_{X|Y}$ has none). In the first case, $I_{\text{acquired}} = I(X; Y)$, while in the two others $I_{\text{acquired}} < I(X; Y)$, as may be proved even without assuming Eq. (1)–(6).

In any case, the value of acquired information is bounded by a mutual information, $I_{\text{acquired}} \leq I(X; Y)$. This mutual information, however, is between the selective pressure X_t and the cue Y_t , both environmental variables, and *not* between the input Y_t and the output Ψ_t of the sensor of a particular individual. The mutual information $I(\Psi; Y)$ can indeed exceed I_{acquired} as shown explicitly with a two-state model in (8) and with a Gaussian model below. The value of acquired information in presence of a sensor with noise $C(\psi|y)$ is

$$I_{\text{acquired}} = I(X; Y) - \min_{\pi_0} \mathbb{E}_Y [D(P_{X|Y}(\cdot|Y) \| \tilde{\pi} * C(\cdot|Y))] + \min_{\pi} D(P_X \| \tilde{\pi}), \quad (20)$$

where $\tilde{\pi} * C(x|y) = \sum_{\phi, \psi} \Delta(x|\phi) \pi_0(\phi|\psi) C(\psi|y)$. A sensor with a given noise $C(\psi|x)$ is in fact always more valuable than an environmental channel $P_{Y|X}$ with same noise (8). This is most simply illustrated with a model with perfect selectivity, as described by Eq. (13). In this case, $Y_t = X_t$ implies $\Lambda = \Lambda^* + \mathbb{E}_X \ln \pi(X|X)$ with $\pi(x|x) = \sum_{\psi} \pi_0(x|\psi) C(\psi|x) = \mathbb{E}_{\Psi|X=x} \pi_0(X|\Psi)$ and, by concavity of the logarithm,

$$\Lambda = \Lambda^* + \mathbb{E}_X \ln \mathbb{E}_{\Psi|X} \pi_0(X|\Psi) \geq \Lambda^* + \mathbb{E}_{X, \Psi} \ln \pi_0(X|\Psi). \quad (21)$$

The right-hand side corresponds to the growth rate of a model with $\Psi_t = Y_t$, where Y_t is given by $P_{Y|X}(y_t|x_t) = C(y_t|x_t)$. This inequality is analogous to the statement in statistical mechanics that the quenched free energy of a disordered system is bounded from below by the corresponding annealed free energy. It represents here the benefice of multiple distributed sensors over a single centralized sensor with same noise.

F. Perfect selectivity

In the other limit of perfect selectivity, an expression formally similar to Eq. (14) can be written

$$\Lambda = \Lambda^* - H(X_1|X_0) + I(X_1; Y_1|X_0) - \mathbb{E}_{X_0, Y_1} [D(P_{X_1|X_0, Y_1}(\cdot|X_0, Y_1) \| \pi(\cdot|X_0, Y_1))], \quad (22)$$

where a conditioning on the past environment X_0 needs to be added (and where π replaces $\tilde{\pi}$). Here, the conditional mutual information $I(X_1; Y_1|X_0)$ is defined by $I(X_1; Y_1|X_0) = H(Y_1|X_0) - H(Y_1|X_1)$ [since $H(Y_1|X_1, X_0) = H(Y_1|X_1)$].

The optimum growth rate is obtained for π minimizing the last term of Eq. (22). In absence of constraints, it is reached for $\hat{\pi} = P_{X_1|X_0, Y_1}$, corresponding to $\hat{\Lambda} = \Lambda^* - H(X_1|X_0) + I(X_1; Y_1|X_0)$. In this case, $I_{\text{acquired}} = I(X_1; Y_1|X_0)$. Since $I(X_1; Y_1|X_0) = I(X_1; Y_1) - I(X_0; X_1)$, the difference with the instantaneous mutual information $I(X_1; Y_1)$, is exactly $I(X_0; Y_1)$, the value of the cue Y_t that is already contained in the knowledge of the past environmental state X_{t-1} . More generally, with constraints, the last term may not vanish and $I_{\text{acquired}} \leq I(X_1; Y_1|X_0)$.

The value of inherited information is read from another equivalent decomposition of the growth rate where X_0 and Y_1 , which play similar roles, are formally exchanged:

$$\Lambda = \Lambda^* - H(X_1|Y_1) + I(X_1; X_0|Y_1) - \mathbb{E}_{X_0, Y_1} [D(P_{X_1|X_0, Y_1}(\cdot|X_0, Y_1) \| \pi(\cdot|X_0, Y_1))]. \quad (23)$$

This implies $I_{\text{inherited}} \leq I(X_1; Y_1|X_0)$, where the conditional mutual information $I(X_0; X_1|Y_1)$ takes into account that some of the information contained in X_{t-1} is also present in Y_t .

Finally, the total information conferred by the two sources of information satisfies

$$I_{\text{tot}} \leq I(X_1; X_0) + I(X_1; Y_1|X_0) = I(X_1; Y_1) + I(X_0; X_1|Y_1), \quad (24)$$

with equality in absence of constraints.

In presence of inheritance, the role of the mutual information is thus played by a conditional mutual information. The conditional mutual information $I(X_1; Y_1|X_0)$ not only differs from the instantaneous mutual information $I(X_1; Y_1)$, but also from the rate of path/trajectory mutual information, which is defined from the mutual information $I(X^t; Y^t)$ between the processes $X^t = (X_1, \dots, X_t)$ and $Y^t = (Y_1, \dots, Y_t)$ as $\lim_{t \rightarrow \infty} I(X^t; Y^t)/t$. The difference becomes apparent when applying the chain rule (6) to write $I(X^t; Y^t) = \sum_{k=1}^t I(X_k; Y^t|X_{k-1})$ since $I(X_k; Y^t|X_{k-1}) \geq$

$I(X_k; Y_k | X_{k-1}) = I(X_1; Y_1 | X_0)$, with, in general, a strict inequality. This inequality accounts for a constraint of causality: an individual has access at time t to the present cue y_t , but not to future cues y_k with $k > t$, which could allow for a better estimation of x_t if available. These considerations extend in non-Markovian environments to strategies of the form $\pi(\phi_t | \phi^{t-1}, y^t)$, where an individual has access to past cues y_k with $k < t$ (14). The value of acquired information then corresponds to the more general concept of directed information, denoted $I(Y \rightarrow X)$, which appears repeatedly in problems of feedback control where constraints of causality are involved (27). The conditional mutual information $I(X_1; Y_1 | X_0)$ is the particular value taken by the directed information $I(Y \rightarrow X)$ when considering stationary, Markovian stochastic processes. The directed information generally differs from the transfer entropy, also proposed to quantify the causal relationships between stochastic processes (28; 29).

III. GAUSSIAN MODEL

We now present a continuous limit of the discrete model for which the growth rate Λ can be computed analytically beyond the two cases of perfect selectivity and no inheritance.

A. Definition

A model with continuous traits $\phi_t \in \mathbb{R}$ is defined by replacing Eq. (2) with

$$n_t(\phi_t) = \frac{1}{W_t} \int d\phi_{t-1} S(\phi_t, x_t) \pi(\phi_t | \phi_{t-1}, y_t) n_{t-1}(\phi_{t-1}), \quad (25)$$

where $n_t(\phi_t)$ represents the density of individuals with trait ϕ_t in the current population, with $n_t(\phi_t) \geq 0$ and $\int d\phi_t n_t(\phi_t) = 1$. The function $S(\phi_t, x_t)$ is chosen as in Eq. (1) to be of a factorized form

$$S(\phi_t, x_t) = K(x_t) G_{\sigma_s^2}(\phi_t - x_t), \quad (26)$$

where $G_{\sigma^2}(x) = (2\pi\sigma^2)^{-1/2} \exp(-x^2/2\sigma^2)$ represents a generic Gaussian function and $K(x) \geq 0$ is arbitrary. We parametrize π as

$$\pi(\phi_t | \phi_{t-1}, y_t) = G_{\sigma_\pi^2}(\phi_t - \lambda\phi_{t-1} - \kappa y_t), \quad (27)$$

where σ_π^2 quantifies the degree of stochasticity, λ the contribution of the inherited information and κ of the acquired information (it can be shown that the optimal π is necessarily of this form).

The growth rate Λ associated with this model can be computed analytically for different environmental processes, but we consider here a stationary Markovian Gaussian process, i.e., a discrete Ornstein-Uhlenbeck process:

$$P_{X_1|X_0}(x_{t+1}|x_t) = G_{\sigma_{x_1|x_0}^2}(x_{t+1} - ax_t), \quad (28)$$

where $a < 1$ parametrizes the temporal correlation between successive environments and $\sigma_{x_1|x_0}^2 = \mathbb{E}[X_1^2|X_0]$ the amplitude of their variations. This interpretation follows from noticing that $\mathbb{E}[X_t X_1] = a^{2t}$ and $\sigma_{x_1}^2 = \mathbb{E}[X_1^2] = \sigma_{x_1|x_0}^2/(1 - a^2)$. Finally, we take a Gaussian channel for $P_{Y_1|X_1} = P_{Y|X}$:

$$P_{Y|X}(y_t|x_t) = G_{\sigma_{y_1|x_1}^2}(y_t - x_t), \quad (29)$$

where $\sigma_{y_1|x_1}^2 = \mathbb{E}[Y_1^2|X_1]$ represents its noise. For independent environments ($a = 0$), this model was studied in (25).

The growth rate Λ for this model can be computed analytically (see Appendix D):

$$\Lambda = \Lambda^* - \frac{1}{2} \ln(2\pi\sigma_s^2) + \frac{1}{2} \ln \frac{\alpha}{\lambda} - \frac{\alpha}{2\lambda(1 - \alpha^2)\sigma_s^2} \left[\frac{(\lambda^2 + (1 - \kappa)^2)(1 + a\alpha) - 2\lambda(1 - \kappa)(a + \alpha)}{(1 - a\alpha)(1 - a^2)} \sigma_{x_1|x_0}^2 + \kappa^2 \sigma_{y_1|x_1}^2 \right], \quad (30)$$

where

$$\alpha = \frac{2\lambda}{1 + \lambda^2 + \beta + ((1 - \lambda^2 - \beta)^2 + 4\beta)^{1/2}}, \quad \beta = \frac{\sigma_\pi^2}{\sigma_s^2}, \quad (31)$$

and $\Lambda^* = \mathbb{E}_X \ln K(X)$. The model has seven parameters, four to describe the environment, σ_s^2 for the selectivity of the environment, a for the correlation between successive environments, $\sigma_{x_1|x_0}^2$ for the amplitude of their fluctuations and $\sigma_{y_1|x_1}^2$ for the (extrinsic) noise of the cue, and three to describe the strategy π : σ_π^2 , λ and κ .

The two limits of no inheritance and perfect selectivity correspond, respectively, to the limits $\lambda \rightarrow 0$ and $\sigma_s^2 \rightarrow 0$. We show below how, in these limits, the growth rate of this continuous model has a decomposition similar to the decomposition of the growth rate of the discrete model. With the continuous Gaussian model, however, explicit formulae for the values of information can be obtained even when they do not coincide with a mutual information. Models with constraints and not assuming any of these limits can also be treated in this same framework (16) [see Appendix G for the link between this model and the model in (16)].

B. No inheritance

In absence of inheritance ($\lambda = 0$), Eq. (30) becomes (see Appendix E):

$$\Lambda = \Lambda^* - h(X) + I(X; Y) - \mathbb{E}_Y[D(P_{X|Y}(\cdot|Y) \|\tilde{\pi}(\cdot|Y))], \quad (32)$$

where $\tilde{\pi}(x|y) = G_{\sigma_s^2} * \pi(x|y) = \int d\phi G_{\sigma_s^2}(\phi - x)\pi(\phi|y) = G_{\sigma_s^2 + \sigma_\pi^2}(x - \kappa y)$ represents an effective strategy as in Eq. (11), and where

$$h(X) = \frac{1}{2} \ln(2\pi e \sigma_{x_1}^2), \quad \text{and} \quad I(X; Y) = \frac{1}{2} \ln \left(1 + \frac{\sigma_{x_1}^2}{\sigma_{y_1|x_1}^2} \right). \quad (33)$$

The only difference with Eq. (14) is the presence of a differential entropy $h(X)$ instead of the entropy $H(X)$. The differential entropy is generally defined for continuous random variables as $h(X) = -\int dx P_X(x) \ln P_X(x)$. While the mutual information $I(X; Y) = h(X) - h(X|Y)$ corresponds to a limit of discrete mutual informations when X is discretized into an increasing number of bits, the discrete entropy diverges in this limit, and the differential entropy $h(X)$ represents only the non-diverging part (6). This divergence is compensated here by the divergence of $S(\phi_t, x_t)$ when $\sigma_s^2 \rightarrow 0$ [see Eq. (26)].

The Gaussian model has the advantage over the discrete model that the value of acquired information I_{acquired} given by Eq. (19) can be evaluated explicitly. If assuming that π is not subject to any additional constraint, three cases must be distinguished (25):

(i) if $\sigma_s^2 \leq \sigma_{x|y}^2$, where $\sigma_{x|y}^2 = (\sigma_x^{-2} + \sigma_{y|x}^{-2})^{-1}$, the two equations $P_{X|Y} = G_{\sigma_s^2} * \pi$ and $P_X = G_{\sigma_s^2} * \pi$ have a solution, respectively given by $\hat{\sigma}_\pi^2 = \sigma_{x|y}^2 - \sigma_s^2$, $\hat{\kappa} = 1/(1 + \sigma_{y|x}^2/\sigma_x^2)$, and $\hat{\sigma}_\pi^2 = \sigma_x^2 - \sigma_s^2$, $\hat{\kappa} = 1$; in this case,

$$I_{\text{acquired}} = I(X; Y) = \frac{1}{2} \ln \left(1 + \frac{\sigma_x^2}{\sigma_{y|x}^2} \right). \quad (34)$$

(ii) if $\sigma_{x|y}^2 < \sigma_s^2 \leq \sigma_x^2$, $P_X = G_{\sigma_s^2} * \pi$ has a solution but not $P_{X|Y} = G_{\sigma_s^2} * \pi$, and $D(P_{X|Y} \| G_{\sigma_s^2} * \pi) > 0$ is minimized with $\hat{\sigma}_\pi^2 = 0$, $\hat{\kappa} = 1/(1 + \sigma_{y|x}^2/\sigma_x^2)$; in this case,

$$I_{\text{acquired}} = I(X; Y) - D(G_{\sigma_{x|y}^2} \| G_{\sigma_s^2}) = \frac{1}{2} \left(\ln \frac{\sigma_x^2}{\sigma_s^2} - \frac{\sigma_{y|x}^2 \sigma_x^2}{(\sigma_{y|x}^2 + \sigma_x^2) \sigma_s^2} + 1 \right). \quad (35)$$

(iii) if $\sigma_s^2 < \sigma_{x|y}^2$, neither $P_{X|Y} = G_{\sigma_s^2} * \pi$ nor $P_X = G_{\sigma_s^2} * \pi$ have solutions and

$$I_{\text{acquired}} = I(X; Y) - D(G_{\sigma_{x|y}^2} \| G_{\sigma_s^2}) + D(G_{\sigma_x^2} \| G_{\sigma_s^2}) = \frac{1}{2} \frac{\sigma_x^4}{(\sigma_{y|x}^2 + \sigma_x^2) \sigma_s^2}. \quad (36)$$

This formulae show how the value of information can depend on the degree of selectivity σ_s^2 of the environment, in addition to the ratio signal/noise $\sigma_x^2/\sigma_{y|x}^2$ that controls the mutual information (Figure 3A).

These different cases are associated with qualitatively different optimal strategies: (i) corresponds to an effective Bayesian strategy, $\tilde{\pi} = P_{X|Y}$, but (ii) and (iii) to a deterministic response, $\hat{\phi}_t = \hat{\kappa} y_t$, also known as a “pure strategy” in game theory. This later case is an example where a Bayesian inference of x_t given y_t is pointless: the optimal strategy is simply to act as if the information was noise-less, with only the multiplication factor $\hat{\kappa}$ to account for the presence of noise.

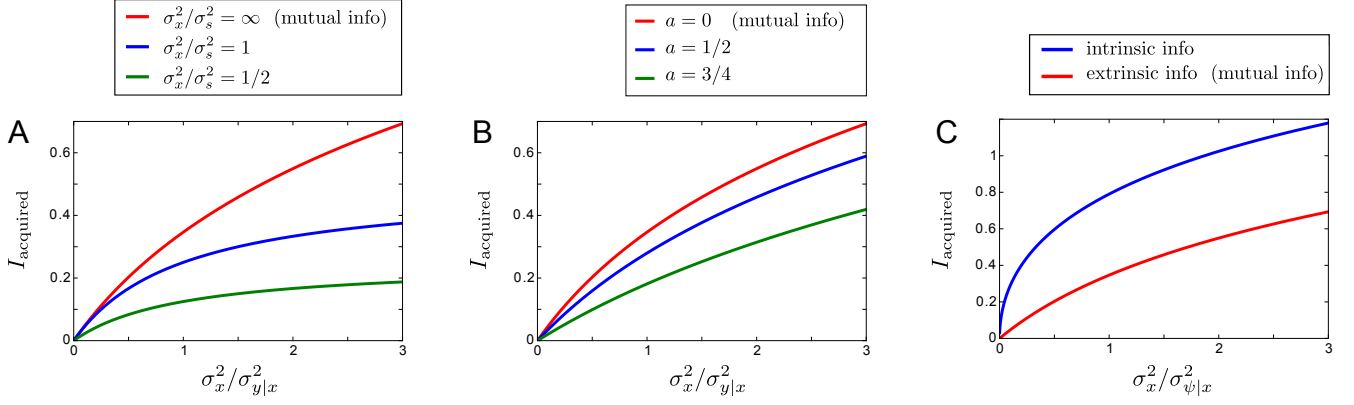


FIG. 3 Value of the acquired information in different limits of the Gaussian model – **A.** No inheritance but finite selectivities σ_s^2 , with $\sigma_s^2 = 0$ (red curve) corresponding to the limit of perfect selectivity where the value of acquired information is given by the mutual information $I(X; Y) = (1/2) \ln(1 + \sigma_x^2/\sigma_{y|x}^2)$. A finite selectivity leads to smaller values for the acquired information (blue and green curves). Here $\sigma_x^2 = \mathbb{E}[X_t^2]$ represents the variance of the selective pressure x_t and $\sigma_{y|x}^2 = \mathbb{E}[Y_t^2|X_t]$ the noise in the environmental cue y_t . **B.** Perfect selectivity but inheritance, with $a = 0$ (red curve) corresponding to the limit where inheritance has no value because the environment has no temporal correlations. In this case, and in this case only, the value of acquired information is given by the mutual information $I(X; Y)$ (red curve), otherwise it has a lower value (blue and green curves). **C.** Extrinsic versus intrinsic informations, with no inheritance and perfect selectivity, but with a possibly noisy individual sensor $C(\psi_t|y_t)$ (as in Figure 2A). When the sensor is noise-less ($\psi_t = y_t$) but the cue y_t has a noise $\sigma_{y|x}^2 = \sigma_{\psi|x}^2$, the value of acquired information is given by the mutual information $I(X; Y)$ (red curve, as in A and B, but note the difference of scale along the y-axis). When the cue is noise-less ($y_t = x_t$) but the sensor has a noise $\sigma_{\psi|x}^2$, the value of acquired information is higher (blue curve).

C. Perfect selectivity

In the limit of perfect selectivity $\sigma_s^2 \rightarrow 0$, we verify that

$$\Lambda = \Lambda^* - h(X_1|X_0) + I(X_1; Y_1|X_0) - \mathbb{E}_Y[D(P_{X|Y}(\cdot|Y) \parallel \pi(\cdot|Y))], \quad (37)$$

which is similar to Eq. (22) but with a conditional differential entropy $h(X_1|X_0)$ instead of the entropy $H(X_1|X_0)$. We have explicitly (see Appendix C):

$$h(X_1|X_0) = \frac{1}{2} \ln(2\pi e \sigma_{x_1|x_0}^2), \quad I(X_1; Y_1|X_0) = \frac{1}{2} \ln \left(1 + \frac{\sigma_{x_1|x_0}^2}{\sigma_{y_1|x_1}^2} \right). \quad (38)$$

Given Eq. (33) and $\sigma_{x_1|x_0}^2 \leq \sigma_{x_1}^2 = \sigma_{x_1|x_0}^2/(1 - a^2)$, we verify that $I(X_1; Y_1|X_0) \leq I(X_1; Y_1)$, with a strict inequality if successive environments are non independent (Figure 3B).

If π is not constrained, the optimal strategy is $\hat{\pi} = P_{X_1|X_0, Y_1}$, which corresponds to (see Appendix C):

$$\hat{\kappa} = \frac{1}{1 + \sigma_{y_1|x_1}^2/\sigma_{x_1|x_0}^2}, \quad \hat{\lambda} = a(1 - \hat{\kappa}), \quad \hat{\sigma}_\pi^2 = \hat{\kappa} \sigma_{x_1|x_0}^2. \quad (39)$$

While the value of acquired information is determined by $I(X_1; Y_1|X_0)$, the value of inherited information is determined by

$$I(X_1; X_0|Y_1) = \frac{1}{2} \ln \left(1 + \frac{\sigma_{x_1|y_1}^2}{\sigma_{x_0|x_1}^2} \right) = \frac{1}{2} \ln \left(1 + a^2 \frac{\sigma_{y_1|x_1}^2}{\sigma_{x_1|x_0}^2} \right). \quad (40)$$

Finally, the total value of the two informations, given in Eq. (24), is at most $I(X_1; Y_1|X_0) + I(X_0; X_1)$, i.e.,

$$I_{\text{tot}} = \frac{1}{2} \ln \left(1 + \frac{\sigma_{x_1|x_0}^2}{\sigma_{y_1|x_1}^2} \right) + \frac{1}{2} \ln \left(\frac{1}{1 - a^2} \right). \quad (41)$$

This formulae show how the value of acquired information depends on the presence of inherited information when the successive environment are correlated ($a > 0$).

D. Common and individual informations

The formulae presented so far assume the absence of constraint on π . They have to be corrected in presence of a noisy individual sensor, as shown by Eq. (20) in absence of inheritance. To illustrate this case in the simplest setting, we assume here both an absence of inheritance ($\lambda = 0$) and an perfect selectivity ($\sigma_s^2 = 0$), in which case Eq. (20) becomes

$$I_{\text{acquired}} = I(X; Y) - \min_{\sigma_\pi^2, \kappa} \mathbb{E}_Y [D(P_{X|Y}(\cdot|Y) \| G_{\sigma_\pi^2 + \kappa^2 \sigma_{\psi|y}^2}(\cdot - \kappa Y))] \quad (42)$$

since $\min_\pi D(P_X \| \pi) = 0$ with $\hat{\pi} = P_X$. Two cases must be distinguished:

- (i) if $\kappa_0^2 \sigma_{\psi|y}^2 \leq \sigma_{x|y}^2$, where $\kappa_0 = 1/(1 + \sigma_{y|x}^2/\sigma_x^2)$ and $\sigma_{x|y}^2 = \kappa_0 \sigma_{y|x}^2$, the equation $P_{X|Y}(x|y) = \pi * G_{\sigma_{\psi|y}^2}(x - \kappa y)$ has a solution given by $\hat{\sigma}_\pi^2 = \sigma_{x|y}^2 - \kappa_0 \sigma_{\psi|y}^2$, $\hat{\kappa} = \kappa_0$, and $I_{\text{acquired}} = I(X; Y)$.
- (ii) if $\kappa_0^2 \sigma_{\psi|y}^2 > \sigma_{x|y}^2$, we have necessarily $D(P_{X|Y} \| \pi * G_{\sigma_{\psi|y}^2}) > 0$, and $\hat{\sigma}_\pi^2 = 0$ but, generally, $\hat{\kappa} \neq \kappa_0$.

An illustration of this second case is provided by a model where $y_t = x_t$ but $\psi_t \neq x_t$, i.e., $\sigma_{y|x}^2 = 0$ and $\sigma_{\psi|y}^2 = \sigma_{\psi|x}^2$. For this particular model, the value of acquired information is (see Appendix F):

$$I_{\text{acquired}} = \frac{1}{2} (\hat{\kappa} - \ln(1 - \hat{\kappa})), \quad \text{with} \quad \hat{\kappa} = \frac{\sqrt{\zeta(\zeta + 4)} - \zeta}{2} \quad \text{and} \quad \zeta = \frac{\sigma_x^2}{\sigma_{\psi|x}^2}. \quad (43)$$

This formula shows that the value of acquired information can be strictly larger than the mutual information between the input and output of the sensor C , since

$$I_{\text{acquired}} \geq I(X; \Psi) = \frac{1}{2} \ln(1 + \zeta) \quad (44)$$

with equality if and only if $\zeta = 0$ (Figure 3C).

IV. FROM EVOLUTIONARY DYNAMICS TO THERMODYNAMICS

The problem of formalizing and quantifying the notion of information also lies at the foundations of thermodynamics. As pointed out by Maxwell in a famous thought experiment, an intelligent being may take advantage of microscopic measurements to extract work from a single heat bath, in apparent contradiction with the second law of thermodynamics (30). Maxwell's demon is today at the center of an active field of research, stochastic thermodynamics, where many results involve information theoretic quantities (24). Recently, Vinkler, Permuter and Merhav showed that the two problems of optimizing the growth rate of a population and optimizing the work extracted from a feedback-controlled thermodynamical system are formally related (23). Here, we present and develop this analogy, first with a simple two-state model, then with more generic discrete and Gaussian models.

A. Simple two-state system

As one of the simplest thermodynamical systems with feedback control, we consider a model where a particle can be in two states, either “down” in potential $V = 0$ or “up” in potential $V = \Delta E > 0$ (Figure 4). The particle is initially at thermal equilibrium with a heat bath at inverse temperature $\beta = 1/(k_B T)$, so that it has probability $p_0 = 1/(1 + e^{-\beta \Delta E})$ to be in the down state, and probability $p_1 = 1 - p_0$ to be in the up state. At regular intervals of time τ , long compared to the equilibration time, a demon can chose to suddenly switch the two levels, thus bringing down the particle if it was up and up if it was down. In doing so, he can extract a work $\mathcal{W} = +\Delta E$ if the particle was in the up state, while losing $\mathcal{W} = -\Delta E$ otherwise. In absence of information on the location of the particle, the expected outcome of the operation is $\mathbb{E}[\mathcal{W}] = (p_1 - p_0)\Delta E < 0$, a negative result in agreement with the impossibility to extract work from a single heat bath. If the demon knows exactly the location of the particle, on the other hand, he can decide to switch the potential only when the particle is in the up state. As it happens with probability p_1 , he can thus expect to extract a positive work, $\mathbb{E}[\mathcal{W}] = p_1 \Delta E > 0$. In the intermediate situation, which we now examine, the demon makes a noisy measurement of the location of the particle and must devise a strategy to optimize the extracted work.

To formalize the problem, let denote by x the state of the particle at the time of a measurement, with $x = 1$ if it is in the up state and $x = 0$ otherwise (Figure 4). Immediately before the demon makes a decision to switch or

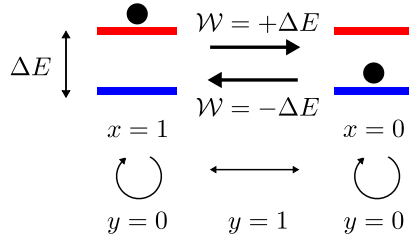


FIG. 4 Optimal control of a two-level system – A particle at equilibrium with a heat bath can be in two states: an up state with energy $+\Delta E$ ($x=1$) or a down state with energy 0 ($x=0$). A measurement is made which indicates, with an error rate $\epsilon < 1/2$, whether the particle is up ($y=1$) or down ($y=0$). Based on this measurement, a demon can choose to switch the two levels, thus extracting a work $\mathcal{W} = +\Delta E$ if the particle was up and performing a work $\mathcal{W} = -\Delta E$ if it was down. To extract a maximal work in average, the optimal strategy of the demon is to switch the two levels if and only if the particle is measured in the up state ($y=1$), as indicated in the bottom.

not the potential, the particle has thus an energy $E_0(x) = x\Delta E$. If $\phi = 1$ denotes the choice to switch the potential and $\phi = 0$ the choice to leave it unchanged, the energy of the particle after making and implementing choice ϕ is $E_1(x|\phi) = |\phi - x|\Delta E$ and the extracted work is $\mathcal{W}(x, \phi) = E_0(x) - E_1(x|\phi) = (2x - 1)\phi\Delta E$. Let now consider the outcome y of a measurement of x , whose noise is characterized by a conditional probability $P_{Y|X}(y|x)$; for instance, $x = y$ with probability $1 - \epsilon$, but $x = 1 - y$ with an error rate ϵ (binary symmetric channel). A strategy choosing ϕ given y with probability $\rho(\phi|y)$ will extract a mean work

$$\mathbb{E}[\mathcal{W}] = \mathbb{E}_{X,Y} \mathbb{E}_{\Phi}[\mathcal{W}(X, \Phi)|Y] = \sum_{x,y,\phi} P_X(x) P_{Y|X}(y|x) \rho(\phi|y) \mathcal{W}(\phi, x), \quad (45)$$

where $P_X(x) = e^{-\beta E_0(x)}/Z_0$ is the equilibrium distribution that describes the particle at the time of the measurement, with $Z_0 = 1 + e^{-\beta\Delta E}$. Because of the linearity of Eq. (45), the question of finding a strategy $\hat{\rho}(\phi|y)$ that optimizes the mean extracted work $\mathbb{E}[\mathcal{W}]$ has a trivial answer: it is simply to switch the potential ($\phi = 1$) if and only if the state $x = 1$ is the most likely given y . With a binary symmetric channel with error rate $\epsilon < 1/2$, this corresponds to the pure strategy $\phi = y$, i.e., $\hat{\rho}(\phi|y) = \delta(\phi, y)$, and results in

$$\mathbb{E}[\mathcal{W}] = \mathbb{E}_{X,Y}[\mathcal{W}(X; Y)|Y] = \sum_{x,y} P_X(x) P_{Y|X}(y|x) \mathcal{W}(y, x). \quad (46)$$

More generally, the outcome of a measurement determines the optimal decision, $\phi = \phi(y)$, and without loss of generality we can assume that the signal directly indicates the optimal choice, $y = \phi$.

An analogy with models of population dynamics arises when introducing the conditional probability $\pi(x|y) = e^{-\beta E_1(x|y)}/Z_1(y)$, where $Z_1(y) = \sum_x e^{-\beta E_1(x|y)}$ (23). Because $Z_1(y) = \sum_x e^{-\beta E_0(x)} = Z_0$ for all y , we can indeed write the extracted work as

$$\mathcal{W}(x, y) = E_0(x) - E_1(x|y) = \beta^{-1} \ln \frac{\pi(x|y)}{P_X(x)}, \quad (47)$$

and, after averaging,

$$\mathbb{E}[\mathcal{W}] = \beta^{-1} \mathbb{E}_{X,Y} \left[\ln \frac{\pi(X|Y)}{P_X(X)} \right]. \quad (48)$$

Up to a multiplying factor β , this expression is formally identical to the expression for the growth rate Λ of a discrete Kelly model given in Eq. (13), with $K(x) = 1/P_X(x)$. This particular value of $K(x)$ has a simple interpretation in gambling: it defines a fair game, with $\hat{\Lambda} = \mathbb{E}_X \ln K(X) - H(X) = 0$. From the standpoint of Kelly's model, the choice of a potential $E_1(x|y)$ thus appears as the choice of a strategy. Following Eq. (18), the mean extracted work satisfies

$$\beta \mathbb{E}[\mathcal{W}] = I(X; Y) - \mathbb{E}_Y[D(P_{X|Y}(\cdot|Y) \parallel \pi(\cdot|Y))]. \quad (49)$$

Irrespectively of the measurement scheme, the extracted work is therefore bounded by the mutual information between the actual and measured locations of the particle: $\beta \mathbb{E}[\mathcal{W}] \leq I(X; Y)$.

B. General discrete systems

Reaching the bound $\beta\mathbb{E}[\mathcal{W}] = I(X;Y)$ requires a potential $E_1(x|y)$ verifying $e^{-\beta E_1(x|y)}/Z_1(y) = P_{X|Y}(x|y)$. This potential, however, need not satisfy $Z_1(y) = Z_0$ for all y . Introducing the free energies $F_0 = -\beta^{-1}\ln Z_0$ and $F_1(y) = -\beta^{-1}\ln Z_1(y)$, the expression for the extracted work when the particle is in x and the measurement indicates y , Eq. (47), generalizes to

$$\mathcal{W}_0(x, y) = E_0(x) - E_1(x|y) = \beta^{-1} \ln \frac{\pi(x|y)}{P_X(x)} + F_0 - F_1(y). \quad (50)$$

In average, the demon will thus extract

$$\mathbb{E}[\mathcal{W}_0] = \beta^{-1} (I(X;Y) - \mathbb{E}_Y[D(P_{X|Y}(\cdot|Y) \parallel \pi(\cdot|Y))]) - \Delta F, \quad (51)$$

where $\Delta F = \mathbb{E}_Y[F_1(Y)] - F_0$. This quantity is analogous to a difference of free energies, but note that the state of the system immediately after the operation is generally not be an equilibrium state. Eq. (51) implies the inequality

$$\mathbb{E}[\mathcal{W}_0] \leq \beta^{-1} I(X;Y) - \Delta F. \quad (52)$$

This inequality corresponds to a known generalization of the second law of thermodynamics in presence of feedback (31). It is more frequently written $\mathbb{E}[\mathcal{W}_0^-] - \Delta F \geq -\beta^{-1} I(X;Y)$, where $\mathcal{W}_0^- = -\mathcal{W}_0$ is the average work *performed* on the system (24). We follow here the opposite convention of counting positively the extracted work for consistency with the sign of the growth rate in the evolutionary model.

To define a cyclic process, the particle needs to be brought back to equilibrium in $E_0(x)$. To this end, the demon has to perform a work $\mathcal{W}_1^-(y) \geq F_0 - F_1(y) + \mathcal{W}_{\text{irr}}^-(y)$ where the irreversible work $\mathcal{W}_{\text{irr}}^-(y) = -\beta^{-1} D(P_{X|Y}(\cdot|y) \parallel \pi(\cdot|y))$ is non-zero when the distribution $P_{X|Y}(x|y)$ of the particle immediately after the measurement differs from the equilibrium distribution in the potential $E_1(x|y)$ (32). This work $\mathcal{W}_1^-(y)$ performed on the system is to be subtracted from the extracted work $\mathcal{W}_0(x, y)$ when estimating the net extracted work over a complete cycle, $\mathcal{W}(x, y) = \mathcal{W}_0(x, y) - \mathcal{W}_1^-(y)$. In average, this results in an extracted work satisfying

$$\beta\mathbb{E}[\mathcal{W}] \leq I(X;Y). \quad (53)$$

This inequality becomes an equality if $\pi = P_{X|Y}$ and the restoration of the original potential is quasi-static, a protocol known to be optimal for discrete-feedback thermodynamic engines (33).

The mapping presented so far is to Kelly's model, which corresponds to taking two limits in the evolutionary model, a limit of perfect selectivity and a limit of no inheritance. We now examine how the analogy may be extended beyond these two limits.

C. Inheritance

Extensions to include inheritance (better called “memory” in this context) are considered in (23). A direct mapping to an evolutionary model with inheritance but perfect selectivity is to assume a multi-step process in which the system is brought back to equilibrium in a new potential $E_0^t(x)$ every time, where $E_0^t(x)$ differs but is correlated to $E_0^{t-1}(x)$. A more interesting extension, however, is to consider that the particle does not equilibrate with the thermal bath before a new measurement and change of potential are made. Physically, equilibration takes time and instead of extracting a maximal work $\mathbb{E}[\mathcal{W}]$, it may be more desirable to extract a maximal power $\mathcal{P} = \mathbb{E}[\mathcal{W}]/\tau$, where τ , the time taken by a cycle, may itself be optimized. We present in Appendix H an extension of Eq. (51) to cover such non-equilibrium protocols. While the extracted work can still be written with information theoretic quantities, their interpretation is complicated by the fact that the state x_t of the system prior to a measurement now depends on the series of choices $\phi^{t-1} = (\phi_1, \dots, \phi_{t-1})$ made by the demon. From the standpoint of the evolutionary model, this corresponds to a feedback from the state of the population to the state of the environment, a biologically relevant phenomenon that could be further studied within the present framework.

D. Finite selectivity

A mapping to an evolutionary model with finite selectivity is for instance obtained by assuming a separation of scales between a macro-state x , which is measured, and micro-states ϕ , which are manipulated, with $S(\phi, x)$ representing

the density of states, i.e., the number of micro-states ϕ associated with the macro-state x . In this mapping, the demon makes a macroscopic measurement of x but, given the result y , can tune every microscopic energy levels from $E_0(\phi)$ to $E_1(\phi|y)$. Assuming that we start and end with the micro-states at equilibrium given their macro-state, Eq. (47) becomes $\mathcal{W}_0(x, y) \leq \mathcal{F}_0(x) - \mathcal{F}_1(x|y)$ where $\mathcal{F}_0(x) = -\beta^{-1} \ln(\sum_{\phi} S(\phi, x) e^{-\beta E_0(\phi)})$ is the free energy of a system at equilibrium in macro-state x , and $\mathcal{F}_1(x|y) = -\beta^{-1} \ln(\sum_{\phi} S(\phi, x) e^{-\beta E_1(\phi|y)})$ at equilibrium in the new distribution of energy levels. By writing again $e^{-\beta E_1(\phi|y)} = \pi(\phi|y) e^{-\beta F_1(y)}$, we obtain

$$\mathcal{W}_0(x, y) \leq \mathcal{F}_0(x) + \beta^{-1} \ln(\sum_{\phi} S(\phi, x) \pi(\phi|y)) - F_1(y), \quad (54)$$

and therefore

$$\mathbb{E}[\mathcal{W}_0] \leq \mathbb{E}_X[\mathcal{F}_0(X)] + \beta^{-1} \mathbb{E}_{X,Y}[\ln(\sum_{\phi} S(\phi, X) \pi(\phi|Y))] - \mathbb{E}_Y[F_1(Y)], \quad (55)$$

with equality if the energy levels are changed quasi-statically. The conditional probability π is involved in the last two terms of the right-hand side, but, as in the two-state model of Figure 4, we may assume that the demon is constrained to $F_1(y) = F_0$ for all y and that the last term is therefore independent of π . In this case, the problem of choosing the energy levels $E_1(\phi|y)$ so as to optimize the extracted work is formally identical to the problem of optimizing the growth rate of an evolutionary model with finite selectivity.

E. Gaussian systems

Mapped to its thermodynamical analog, the Gaussian model of evolutionary dynamics becomes the problem of controlling a Brownian particle with harmonic potentials. The Gaussian distribution $P_X(x) = G_{\sigma_x^2}(x)$ is indeed the equilibrium distribution of a particle in contact with an heat bath at inverse temperature β and in a potential $V_0(x) = kx^2/2$ when considering $\sigma_x^2 = (\beta k)^{-1}$. In the simplest version of the analogy, a demon observes a particle at equilibrium in this potential and measures its location x at y , with a noise characterized by $P_{Y|X}(y|x) = G_{\sigma_{y|x}^2}(y-x)$. His problem is then to change the potential to $V_1(x|y)$ so as to extract a maximal work.

While changing the stiffness k of the potential may allow the demon to extract more work, the simplest scenario is when only translations are allowed, from $V_0(x) = kx^2/2$ to $V_1(x|y) = k(x - \phi_1)^2/2$, a case where $Z_1(y) = Z_0 = (2\pi\sigma_x^2)^{1/2}$, and therefore $\Delta F = 0$ in Eq. (51). As a consequence of the formal mapping to an evolutionary model, the optimal strategy of the demon is to move the potential to $\phi_1 = \hat{\kappa} y_0$ with $\hat{\kappa}$ given by Eq. (39), i.e., $\hat{\kappa} = 1/(1 + \sigma_{y|x}^2/\sigma_x^2)$. The optimal extracted work is the value of acquired information given by Eq. (35) when taking $\sigma_s^2 = \sigma_x^2$: $\mathbb{E}[\hat{W}] = (1 - \sigma_{x|y}^2/\sigma_x^2)/2 = (1 + \sigma_{y|x}^2/\sigma_x^2)^{-1}/2$. These expressions corresponds to those obtained by a more direct calculation (34).

If the process is repeated after quasi-statically restoring the potential at a location that is correlated but differs from its original location, the problem maps to the Gaussian model of evolutionary dynamics with inheritance. Specifically, it corresponds to beginning each cycle t with the particle at equilibrium in $V_t(x) = k(x - x_t)^2/2$, where $x_t = ax_{t-1} + \nu_t$ and where ν_t is normally distributed with variance $\sigma_{x_1|x_0}^2$. This problem also maps to a problem of stochastic control solved by Kalman (22). In Kalman's model, the state x_t of a system, its measured state y_t and its estimated state ϕ_t are assumed to follow the recursions

$$x_t = ax_{t-1} + \nu_t, \quad \nu_t \sim \mathcal{N}(0, \sigma_{x_1|x_0}^2), \quad (56)$$

$$y_t = x_t + \nu'_t, \quad \nu'_t \sim \mathcal{N}(0, \sigma_{y_1|x_1}^2), \quad (57)$$

$$\phi_t = \lambda\phi_{t-1} + \kappa y_t, \quad (58)$$

and the objective is to find the estimation ϕ_t that minimizes the mean square error $\mathbb{E}[(\phi_t - x_t)^2]$ by choosing appropriately the two parameters λ and κ . A standard application is for instance to tracking, where the current position and velocity of a target must be estimated from past estimations and from independent measurements. The optimal values for $\hat{\lambda}$ and $\hat{\kappa}$ are also given by Eq. (39) (as for our model, a generalization to multidimensional variables is straightforward).

A physically more interesting situation is when the particle has no time to equilibrate before a new measurement and manipulation are made. The Gaussian setting is here again well-suited for making explicit calculations of the

maximal work that may be extracted with such non-equilibrium protocols (35) (see also Appendix H). The results obtained for Brownian particles in harmonic potentials suggest that the feedback of a population onto its environment could also be studied analytically in Gaussian models of population dynamics.

V. DISCUSSION

We reviewed an approach to quantify the value of informations in evolution by analyzing abstract models of population dynamics, and showed how analytical expressions can be obtained when considering a particular Gaussian limit. This approach illustrates how the value of an information may depend on factors beyond the characteristics of the channel that directly conveys it. In particular, it shows how the value of an information acquired from the current environment is tied to the value of the information inherited from previous generations. Alternative approaches for quantifying information are possible, for instance based on well-chosen sets of axioms (36), but at the risk of omitting an important feature of the problem. Although elementary, our model indicates that several constraints should generically be taken into account, including causality, selectivity of the environment and individual stochasticity. Studies of informations in thermodynamics take a similar approach of analyzing simple models and also find that different quantities for quantifying information may arise depending on the protocol (37). Remarkably, a similar mathematical formalism emerges from the two problems (23).

This formal correspondence suggests that methods and concepts may be transferred between disciplines. In (23), the authors thus applied the concept of universal strategy from information theory (38) to devise a thermodynamical protocol that optimally extracts work when the statistical properties of the system, for instance the characteristics of the information channel, are unknown. Reciprocally, many results have been obtained recently in stochastic thermodynamics (24) which may provide new insights on evolutionary dynamics. For instance, inequalities on the mean extracted work are known to generalize to fluctuation theorems, which take into account fluctuations around the mean result and connect macroscopic observations to the underlying time-reversal symmetry of the microscopic dynamics. Given the analogy between extracted work and growth rate, similar relations may hold for population dynamics. One such fluctuation relation has in fact already been established for evolutionary dynamics by Mustonen and Lässig (39), but at a different level of analysis: they considered fluctuations arising from finite population sizes, which are ignored in the present analysis of our models. The path integral formalism at the core of their approach has, however, its counterpart at our level of analysis (12).

Another challenge is to move beyond the formal analogy towards an integrated treatment of evolutionary and thermodynamical constraints. The presented models account for part of the evolutionary constraints but the information processor π , the sensor C and the “replicator” S are introduced as ad-hoc parameters, with no reference to physics or evolution. Several recent studies have investigated thermodynamical constraints on information processing (40), biochemical sensing (41) or replication (42), and others have investigated evolutionary constraints at the inter-molecular (43) and intra-molecular (44) levels. Given the interplay between local and global properties that simple models already exhibit, integrating these different constraints appears as both necessary and interesting.

Acknowledgments

I thank B. Houchmandzadeh and M. Ribezzi for helpful comments.

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APPENDICES

Appendix A: Mapping from Eq. (6) to Eq. (2)

The model described by Eq. (6) is mapped to the model described by Eq. (2) by defining

$$\tilde{\phi}_t = (\gamma_t, \phi_t), \quad \tilde{x}_t = (0, x_t), \quad \tilde{y}_t = (y_t, z_t) \quad (\text{A1})$$

and

$$\pi(\tilde{\phi}_t | \tilde{\phi}_{t-1}, \tilde{y}_t) = H(\tilde{\phi}_t^1 | \tilde{\phi}_{t-1}^1, \tilde{\phi}_t^2, \tilde{y}_t^2) D(\tilde{\phi}_t^2 | \tilde{\phi}_{t-1}^1, \tilde{y}_t^1), \quad \tilde{S}(\tilde{\phi}_t, \tilde{x}_t) = S(\tilde{\phi}_t^2, \tilde{x}_t^2), \quad (\text{A2})$$

where $\tilde{\phi}_t^k$ corresponds to the k -th component of $\tilde{\phi}_t$, i.e., $\tilde{\phi}_t = (\tilde{\phi}_t^1, \tilde{\phi}_t^2)$. Note that \tilde{S} is of the form $\tilde{S} = \tilde{K} \tilde{\Delta}$ as in Eq. (1) if S is itself of the form $S = K \Delta$.

Appendix B: Decomposition of the growth rate

We detail here the decomposition of the growth rate given in Eq. (14) for the discrete model in absence of inheritance. The idea is to write

$$\begin{aligned} \Lambda &= \mathbb{E}_{X,Y} [\ln(K(X) \tilde{\pi}(X|Y))] \\ &= \mathbb{E}_{X,Y} [\ln(K(X))] + \mathbb{E}_{X,Y} [\ln P_X(x)] + \mathbb{E}_{X,Y} \left[\ln \frac{P_{X|Y}(X|Y)}{P_X(X)} \right] + \mathbb{E}_{X,Y} \left[\ln \frac{\tilde{\pi}(X|Y)}{P_{X|Y}(X|Y)} \right], \end{aligned} \quad (\text{B1})$$

and to recognize that $\mathbb{E}_{X,Y} [\ln P_X(x)] = -H(X)$, $\mathbb{E}_{X,Y} [\ln P_{X|Y}(X|Y)/P_X(X)] = I(X; Y)$ and

$$\begin{aligned} \mathbb{E}_{X,Y} \left[\ln \frac{\tilde{\pi}(X|Y)}{P_{X|Y}(X|Y)} \right] &= \sum_{x,y} P_{X,Y}(x,y) \ln \frac{\tilde{\pi}(x|y)}{P_{X|Y}(x|y)} = \sum_y P_Y(y) \sum_x P_{X|Y}(x|y) \ln \frac{\tilde{\pi}(x|y)}{P_{X|Y}(x|y)} \\ &= - \sum_y P_Y(y) D(P_{X|Y}(\cdot|y) \| \tilde{\pi}(\cdot|y)) = -\mathbb{E}_Y [D(P_{X|Y}(\cdot|Y) \| \tilde{\pi}(\cdot|Y))]. \end{aligned} \quad (\text{B2})$$

Appendix C: Gaussian random variables

A Gaussian random variable X is characterized by its mean $x_0 = \mathbb{E}[X]$ and its variance $\sigma_x^2 = \mathbb{E}[X^2] - \mathbb{E}[X]^2$, and its probability density is $P_X(x) = G_{\sigma_x^2}(x - x_0)$, where $G_{\sigma_x^2}(x) = (2\pi\sigma_x^2)^{-1/2} \exp(-x^2/2\sigma_x^2)$.

Its differential entropy $h(X) = -\int dx P_X(x) \ln P_X(x)$ is

$$h(X) = \frac{1}{2} \ln(2\pi e \sigma_x^2). \quad (\text{C1})$$

The mutual information $I(X; Y) = h(X) - h(X|Y)$ between X and another Gaussian random variable Y whose conditional probability given x is $P_{Y|X}(y|x) = G_{\sigma_{y|x}^2}(y - x)$ is

$$I(X; Y) = \frac{1}{2} \ln \left(1 + \frac{\sigma_x^2}{\sigma_{y|x}^2} \right). \quad (\text{C2})$$

The relative entropy between two Gaussian probability densities is

$$D(G_{\sigma_0^2}(\cdot - x_0) \| G_{\sigma_1^2}(\cdot - x_1)) = \frac{1}{2} \left(\frac{\sigma_0^2 + (x_1 - x_0)^2}{\sigma_1^2} - \ln \frac{\sigma_0^2}{\sigma_1^2} - 1 \right). \quad (\text{C3})$$

Finally, given $P_{X_1|X_0}(x_1|x_0) = G_{\sigma_{x_1|x_0}^2}(x_1 - ax_0)$ and $P_{Y_1|X_1}(y_1|x_1) = G_{\sigma_{y_1|x_1}^2}(y_1 - x_1)$, the conditional probability $P_{X_1|Y_1, X_0}$, which by Bayes' rule is proportional to $P_{Y_1|X_1}P_{X_1|X_0}$, is also Gaussian and given by

$$P_{X_1|Y_1, X_0}(x_1|y_1, x_0) = G_{\sigma_{x_1|y_1, x_0}^2}(x_1 - \lambda x_0 - \kappa y_1), \quad (\text{C4})$$

with

$$\kappa = \frac{1}{1 + \sigma_{y_1|x_1}^2/\sigma_{x_1|x_0}^2}, \quad \lambda = a(1 - \kappa), \quad \sigma_{x_1|y_1, x_0}^2 = \kappa \sigma_{x_1|x_0}^2, \quad (\text{C5})$$

or, equivalently, $\sigma_{x_1|y_1, x_0}^{-2} = \sigma_{x_1|x_0}^{-2} + \sigma_{y_1|x_1}^{-2}$.

Appendix D: Growth rate of the Gaussian model

Eq. (30) for the growth rate Λ of the Gaussian model is obtained by considering

$$n_t(\phi_t) = \frac{1}{W_t} K(x_t) \int d\phi_{t-1} G_{\sigma_s^2}(\phi_t - x_t) G_{\sigma_\pi^2}(\phi_t - \lambda \phi_{t-1} - \kappa y_t) n_t(\phi_{t-1}), \quad (\text{D1})$$

with $n_t(\phi_t)$ of the form $n_t(\phi_t) = G_{\sigma_t^2}(\phi_t - m_t)$, which leads to

$$m_t = \frac{\sigma_s^2}{\sigma_s^2 + \sigma_\pi^2 + \lambda^2 \sigma_{t-1}^2} (\lambda m_{t-1} + \kappa y_t) + \frac{\sigma_\pi^2 + \lambda^2 \sigma_{t-1}^2}{\sigma_s^2 + \sigma_\pi^2 + \lambda^2 \sigma_{t-1}^2} x_t \quad (\text{D2})$$

$$\sigma_t^2 = (\sigma_s^{-2} + (\sigma_\pi^2 + \lambda^2 \sigma_{t-1}^2)^{-1})^{-1} \quad (\text{D3})$$

$$W_t = K(x_t) G_{\sigma_s^2 + \sigma_\pi^2 + \lambda^2 \sigma_{t-1}^2}(\lambda m_{t-1} - x_t + \kappa y_t). \quad (\text{D4})$$

The variance σ_t^2 has a fixed point σ_∞^2 in terms of which the growth rate can be rewritten as

$$\Lambda = \lim_{t \rightarrow \infty} \mathbb{E}[\ln W_t] = \Lambda^* - \frac{1}{2} \ln(2\pi \sigma_s^2) + \frac{1}{2} \ln \frac{\alpha}{\lambda} - \frac{\alpha}{2\lambda \sigma_s^2} \lim_{t \rightarrow \infty} \mathbb{E}[z_t^2], \quad (\text{D5})$$

where $\Lambda^* = \mathbb{E}_X[\ln K(X)]$,

$$z_t = \lambda m_{t-1} - x_t + \kappa y_t, \quad (\text{D6})$$

and

$$\alpha = \frac{\lambda \sigma_s^2}{\sigma_s^2 + \sigma_\pi^2 + \lambda^2 \sigma_\infty^2} = \frac{2\lambda}{1 + \lambda^2 + \beta + ((1 - \lambda^2 - \beta)^2 + 4\beta)^{1/2}}, \quad \text{with } \beta = \frac{\sigma_\pi^2}{\sigma_s^2}. \quad (\text{D7})$$

Given that $x_{t+1} = ax_t + b_t$ and $y_{t+1} = x_{t+1} + b'_{t+1}$ with $b_t \sim \mathcal{N}(0, \sigma_{x_1|x_0}^2)$ and $b'_{t+1} \sim \mathcal{N}(0, \sigma_{y_1|x_1}^2)$, we have

$$z_{t+1} = \alpha z_t + \epsilon x_t + (\kappa - 1)b_t + \kappa b'_{t+1}, \quad \text{with } \epsilon = \lambda - a(1 - \kappa). \quad (\text{D8})$$

Using $\sum_{k=0}^t \alpha^{t-k} x_k = \sum_{k=0}^t (\alpha^{t-k} - a^{t-k})/(\alpha - a) b_k$, we obtain

$$z_{t+1} = \frac{1}{\alpha - a} \sum_{k=0}^t (\delta \alpha^{t-k} - \epsilon a^{t-k}) b_k + \kappa \sum_{k=0}^t \alpha^{t-k} b'_{k+1}, \quad \text{with } \delta = \lambda - \alpha(1 - \kappa), \quad (\text{D9})$$

and, since the b_k and b'_k are all independent, with variances $\mathbb{E}[b_k^2] = \sigma_{x_1|x_0}^2$ and $\mathbb{E}[b'_k{}^2] = \sigma_{y_1|x_1}^2$,

$$\lim_{t \rightarrow \infty} \mathbb{E}[z_{t+1}^2] = \frac{1}{(\alpha - a)^2} \left(\frac{\delta^2}{1 - \alpha^2} - \frac{2\delta\epsilon}{1 - a\alpha} + \frac{\epsilon^2}{1 - a^2} \right) \sigma_{x_1|x_0}^2 + \kappa^2 \frac{\sigma_{y_1|x_1}^2}{1 - \alpha^2} \quad (\text{D10})$$

$$= \frac{(\lambda^2 + (1 - \kappa)^2)(1 + a\alpha) - 2\lambda(1 - \kappa)(a + \alpha)}{(1 - \alpha^2)(1 - a\alpha)(1 - a^2)} \sigma_{x_1|x_0}^2 + \kappa^2 \frac{\sigma_{y_1|x_1}^2}{1 - \alpha^2}. \quad (\text{D11})$$

Plugged into Eq. (D5), it leads to Eq. (30).

Appendix E: Decomposition of the growth rate of the Gaussian model

Since the Gaussian model can be obtained as a continuous limit of the discrete model, Eqs. (32)-(37) directly result from Eqs. (14)-(22) by taking the same limit. The decomposition can also be derived directly from the general formula of Eq. (30) as we illustrate it here in the simplest case where the two limits are taken.

The first limit, of perfect selectivity, corresponds to $\sigma_s^2 \rightarrow 0$, such that Eq. (30) becomes

$$\Lambda = \Lambda^* - \frac{1}{2} \ln(2\pi\sigma_\pi^2) - \frac{1}{2\sigma_\pi^2} \left[\frac{\lambda^2 + (1-\kappa)^2 - 2\lambda(1-\kappa)a}{1-a^2} \sigma_{x_1|x_0}^2 + \kappa^2 \sigma_{y_1|x_1}^2 \right]. \quad (\text{E1})$$

The second limit, of no inheritance, simply corresponds to setting $\lambda = 0$ in this equation, so that

$$\Lambda = \Lambda^* - \frac{1}{2} \ln(2\pi\sigma_\pi^2) - \frac{1}{2\sigma_\pi^2} \left[(1-\kappa)^2 \sigma_{x_1}^2 + \kappa^2 \sigma_{y_1|x_1}^2 \right], \quad (\text{E2})$$

where $\sigma_{x_1}^2 = \sigma_{x_1|x_0}^2 / (1-a^2)$ represents the stationary variance of the environmental process, $\sigma_{x_1}^2 = \mathbb{E}[X_1^2]$. The optimal strategy $\hat{\pi}$ is obtained by optimizing Λ over κ and σ_π^2 , which leads to

$$\hat{\kappa} = \frac{1}{1 + \sigma_{y_1|x_1}^2 / \sigma_{x_1}^2}, \quad \hat{\sigma}_\pi^2 = \hat{\kappa} \sigma_{y_1|x_1}^2. \quad (\text{E3})$$

$\hat{\kappa}$ can also be written $\hat{\kappa} = \sigma_{x_1}^2 / \sigma_{y_1}^2$ where $\sigma_{y_1}^2 = \sigma_{x_1}^2 + \sigma_{y_1|x_1}^2$ represents the stationary variance of y_t . As expected from the analysis of the discrete model, we verify that the optimal strategy implements a Bayesian estimation, i.e., $\hat{\pi} = P_{X|Y}$ [see Appendix C]. We also verify that the optimal optimal growth rate,

$$\hat{\Lambda} = \Lambda^* - \frac{1}{2} \ln \left(2\pi \frac{\sigma_{y_1|x_1}^2 \sigma_{x_1}^2}{\sigma_{x_1}^2 + \sigma_{y_1|x_1}^2} \right) - \frac{1}{2}, \quad (\text{E4})$$

is equivalently written

$$\hat{\Lambda} = \Lambda^* - h(X) + I(X; Y), \quad (\text{E5})$$

where

$$h(X) = \frac{1}{2} \ln(2\pi e \sigma_{x_1}^2), \quad \text{and} \quad I(X; Y) = \frac{1}{2} \ln \left(1 + \frac{\sigma_{x_1}^2}{\sigma_{y_1|x_1}^2} \right). \quad (\text{E6})$$

More generally, by introducing $\sigma_{x_1|y_1}^{-2} = \sigma_{y_1|x_1}^{-2} + \sigma_{x_1}^{-2}$, so that $(1-\kappa)^2 \sigma_{x_1}^2 + \kappa^2 \sigma_{y_1|x_1}^2 = \sigma_{x_1|y_1}^2 + (\hat{\kappa} - \kappa)^2 \sigma_{y_1}^2$, we verify that Eq. (E2) is equivalent to

$$\Lambda = \hat{\Lambda} - \frac{1}{2} \left[\frac{\sigma_{x_1|y_1}^2 + (\hat{\kappa} - \kappa)^2 \sigma_{y_1}^2}{\sigma_\pi^2} - \ln \frac{\sigma_{x_1|y_1}^2}{\sigma_\pi^2} - 1 \right] = \hat{\Lambda} - \mathbb{E}_Y [D(P_{X|Y}(\cdot|Y) \| \pi(\cdot|Y))], \quad (\text{E7})$$

as expected from Eq. (13).

Appendix F: Gaussian model with individual sensors

Using the formulae of Appendix C, the term to maximize in Eq. (42) can be written

$$I(X; Y) - \mathbb{E}_Y [D(P_{X|Y} \| G_{\sigma_\pi^2 + \kappa^2 \sigma_{\psi|y}^2}(\cdot - \kappa Y))] = \frac{1}{2} \ln \left(1 + \frac{\sigma_x^2}{\sigma_{y|x}^2} \right) - \frac{1}{2} \left(\frac{\sigma_{x|y}^2 + (\kappa - \kappa_0)^2 \sigma_y^2}{\sigma_\pi^2 + \kappa^2 \sigma_{\psi|y}^2} - \ln \frac{\sigma_{x|y}^2}{\sigma_\pi^2 + \kappa^2 \sigma_{\psi|y}^2} - 1 \right). \quad (\text{F1})$$

When $Y \rightarrow X$, $\kappa_0 \rightarrow 1$, $\sigma_y^2 \rightarrow 0$, $\sigma_{y|x}^2 \rightarrow 0$ and $\sigma_{x|y}^2 \rightarrow 0$ but $\sigma_{x|y}^2 / \sigma_{y|x}^2 \rightarrow 1$ and it simplifies to

$$\frac{1}{2} \left[\ln \left(\frac{\sigma_x^2}{\sigma_\pi^2 + \kappa^2 \sigma_{\psi|x}^2} \right) - \frac{(\kappa - 1)^2 \sigma_x^2}{\sigma_\pi^2 + \kappa^2 \sigma_{\psi|x}^2} + 1 \right]. \quad (\text{F2})$$

The maximum over σ_π^2 is reached for $\sigma_\pi^2 = 0$ and taking the derivative with respect to κ leads to

$$\kappa^2 \sigma_{\psi|x}^2 + (\kappa - 1) \sigma_x^2 = 0 \quad (\text{F3})$$

whose solution is given in Eq. (43).

Appendix G: The Gaussian model as a limit of the general model of Ref. (16)

A general model is defined by Eqs. [S1]-[S2] in the Supporting Information of (16), which we repeat here with only slightly modified notations:

$$\gamma'_0 = \lambda_0 \gamma_0 + \kappa_0 z_t + \omega_0 \phi_0 + \nu_H, \quad \nu_H \sim \mathcal{N}(0, \sigma_H^2), \quad (\text{G1})$$

$$\phi_0 = \theta_0 \gamma_0 + \rho_0 y_t + \nu_D, \quad \nu_D \sim \mathcal{N}(0, \sigma_D^2), \quad (\text{G2})$$

$$S(\phi_0, x_t) = \exp[r_{\max} - (\phi_0 - x_t)^2 / (2\sigma_s^2)], \quad (\text{G3})$$

$$x_t = ax_{t-1} + b_t, \quad b_t \sim \mathcal{N}(0, \sigma_{x_1|x_0}^2), \quad (\text{G4})$$

$$y_t = x_t + b'_t, \quad b'_t \sim \mathcal{N}(0, \sigma_{y|x}^2), \quad (\text{G5})$$

$$z_t = x_t + b''_t, \quad b''_t \sim \mathcal{N}(0, \sigma_{z|x}^2). \quad (\text{G6})$$

$$(\text{G7})$$

Without loss of generality it can be assumed that $\sigma_s^2 = 1$. The formula for the growth rate of this general model is given with an error in Eq. [S3] of (16). The correct formula is

$$\Lambda = r_{\max} + \frac{1}{2} \ln \frac{\alpha}{\eta} - \frac{\alpha}{2\eta(1-\alpha^2)} \left[\frac{(v^2 + (1-\rho_0)^2)(1+a\alpha) - 2v(1-\rho_0)(a+\alpha)}{1-a\alpha} \sigma_x^2 + \rho_0^2(1-2\alpha\lambda_0 + \lambda_0^2) \sigma_{y|x}^2 + \kappa_0^2 \theta_0^2 \sigma_{z|x}^2 \right], \quad (\text{G8})$$

where $\sigma_x^2 \equiv \sigma_{x_1|x_0}^2 / (1-a^2)$, where η and v given by

$$\eta = \lambda_0(1 + \sigma_D^2) + \omega_0 \theta_0, \quad v = (\omega_0 + \kappa_0) \theta_0 + (1 - \rho_0) \lambda_0, \quad (\text{G9})$$

and

$$\alpha = \frac{2\tilde{\lambda}}{1 + \tilde{\lambda}^2 + \tilde{\sigma}_H^2 + \left((1 - \tilde{\lambda}^2 - \tilde{\sigma}_H^2)^2 + 4\tilde{\sigma}_H^2 \right)^{1/2}}, \quad (\text{G10})$$

with

$$\tilde{\sigma}_H^2 = \left(\sigma_H^2 + \frac{\omega_0^2 \sigma_D^2}{\sigma_D^2 + 1} \right) \frac{\theta_0^2}{\sigma_D^2 + 1}, \quad \tilde{\lambda} = \lambda_0 + \frac{\theta_0 \omega_0}{\sigma_D^2 + 1} \quad (\text{G11})$$

These formulae reduce to Eq. (30) when taking $\theta_0 = \lambda$, $\rho_0 = \kappa$, $\omega_0 = 1$, $\sigma_D^2 = \sigma_\pi^2$, $\lambda_0 = \kappa_0 = \sigma_H^2 = \sigma_{z|x}^2 = 0$ and $r_{\max} = \ln K - (1/2) \ln(2\pi\sigma_s^2)$.

Appendix H: Feedback control out of equilibrium

The state x_t of a system in contact with a heat bath is measured as y_t at regular intervals of time τ , upon which the potential in which the system evolves is changed from $V_{t-1}(x)$ to $V_t(x)$. This change is done without knowing the current state x_t , but may depend on the history of past measurements $y^t = (y_1, \dots, y_t)$ as well as on the history of past states at the time of these measurements, $x^{t-1} = (x_1, \dots, x_{t-1})$. If we assume that the potential is controllable by one or several parameters ℓ , we therefore consider, in the more general case, that $\ell_t = \ell(y^t, x^{t-1})$ [in more constrained cases, ℓ_t may depend only on some of variables, e.g., $\ell_t = \ell(y^t)$ when only the present and past measurements are available]. In-between two measurements, the system relaxes in a constant potential $V_t(x)$ but may not reach equilibrium; its dynamics is generally stochastic, due to the interaction with the heat bath, and may for instance be described by a Master equation with rates satisfying detailed balance. When changing the potential from $V_{t-1}(x)$ to $V_t(x)$, a demon extracts a work $\mathcal{W}_t = V_{t-1}(x_t) - V_t(x_t)$. The goal of the demon is either to optimize the total extracted work $\mathcal{W}_{\text{tot}} = \mathbb{E}[\sum_t \mathcal{W}_t]$ or, if τ itself is controllable, to optimize the power $\mathcal{W}_{\text{tot}}/\tau$.

To formalize this problem, we denote by $p_{t-1}^\tau(x_t)$ the probability of the system to be in state x_t at the time of the t -th measurement: this probability depends explicitly only on ℓ_{t-1} and x_{t-1} , which characterize, respectively, the potential $V_{t-1}(x)$ and the state of the system when this potential is switched on. Introducing $F_t = -\beta^{-1} \ln \sum_x e^{-\beta V_t(x)}$ and $p_t^{(\infty)}(x) = e^{\beta[F_t - V_t(x)]}$ (also denoted π in the main text), the extracted work may be decomposed as

$$\mathcal{W}_t(x^t, y^t) = V_{t-1}(x_t) - V_t(x_t) = \beta^{-1} \ln \frac{p_t^{(\infty)}(x_t)}{p_{t-1}^\tau(x_t)} + \beta^{-1} \ln \frac{p_{t-1}^\tau(x_t)}{p_{t-1}^{(\infty)}(x_t)} - (F_t - F_{t-1}). \quad (\text{H1})$$

We now consider the past history (x^{t-1}, y^{t-1}) as given and average over (X_t, Y_t) to define

$$\mathbb{E}_t[\mathcal{W}_t] = \mathbb{E}_{X_t, Y_t | X^{t-1}=x^{t-1}, Y^{t-1}=y^{t-1}}[\mathcal{W}_t(X^t, Y^t)]. \quad (\text{H2})$$

Since $P_{X_t | X^{t-1}, Y^{t-1}}(x_t | x^{t-1}, y^{t-1}) = p_{t-1}^\tau(x_t)$, we have

$$\beta \mathbb{E}_t[\mathcal{W}_t] = I(X_t; Y_t | x^{t-1}, y^{t-1}) - \mathbb{E}[D(q_{t-1}^\tau \| p_t^\infty)] + \mathbb{E}[D(p_{t-1}^\tau \| p_{t-1}^\infty)] - \beta \mathbb{E}[F_t - F_{t-1}], \quad (\text{H3})$$

where

$$q_{t-1}^\tau(x_t | y_t) = P_{X_t | X^{t-1}, Y^t}(x_t | x^{t-1}, y^t) = \frac{P_{Y|X}(y_t | x_t) p_{t-1}^\tau(x_t)}{\sum_x P_{Y|X}(y_t | x) p_{t-1}^\tau(x)} \quad (\text{H4})$$

and

$$I(X_t; Y_t | x^{t-1}, y^{t-1}) = \sum_{x_t, y_t} P_{Y|X}(y_t | x_t) p_{t-1}^\tau(x_t) \ln \frac{q_{t-1}^\tau(x_t | y_t)}{p_{t-1}^\tau(x_t)} \quad (\text{H5})$$

The total work \mathcal{W}_{tot} is obtained as $\mathcal{W}_{\text{tot}} = \sum_t \mathbb{E}_{X^{t-1}, Y^{t-1}}[\mathbb{E}_t[\mathcal{W}_t]]$. When $\tau \rightarrow \infty$, the third term on the right-hand side of Eq. (H3) vanishes and we recover the equilibrium result, Eq. (51).

This formalism can be applied to a Brownian particle in a controllable harmonic potential. For simplicity, we assume that only the location of the potential can be controlled, and its stiffness k is fixed to $k = 1$. We also set $\beta = 1$. The potential $V_t(x) = (x - \ell_t)^2/2$ is characterized by the location ℓ_t of its minimum, and $F_t = F_{t-1}$ for all t . We take the relaxation dynamics between measurements to be described by a Fokker-Planck equation,

$$\partial_\tau p_t^\tau(x) = \partial_x(\partial_x V_t(x) p_t^\tau(x)) + \partial_x^2 p_t^\tau(x), \quad (\text{H6})$$

with the initial condition is $p_t^0(x) = \delta(x - x_t)$. This equation is easily solved as its solution is Gaussian at all time: $p_t^\tau(x) = G_{\varsigma_\tau^2}(x - \mu_t^\tau)$ with

$$\frac{1}{2} \partial_\tau \mu_t^\tau + \mu_t^\tau = \ell_t, \quad \mu_t^0 = x_t, \quad (\text{H7})$$

$$\frac{1}{2} \partial_\tau \varsigma_\tau^2 + \varsigma_\tau^2 = 1, \quad \varsigma_0^2 = 0, \quad (\text{H8})$$

so that

$$\mu_t^\tau = (1 - e^{-\tau}) \ell_t + e^{-\tau} x_t, \quad (\text{H9})$$

$$\varsigma_\tau^2 = 1 - e^{-2\tau}. \quad (\text{H10})$$

When $\tau \rightarrow \infty$, $p_t^\tau(x)$ converges to the equilibrium distribution $p_t^\infty(x) = G_1(x - \ell_t)$. Using $P_{Y|X}(y_t | x_t) = G_{\sigma_{y|x}^2}(y_t - x_t)$ and applying Eq. (C4), q_t^τ is found to be

$$q_{t-1}^\tau(x_t | y_t) = G_{\sigma_{x|y}^2}(x_t - (1 - \kappa) \mu_{t-1}^\tau - \kappa y_t), \quad \text{with } \kappa = \frac{1}{1 + \sigma_{y|x}^2 / \varsigma_\tau^2}, \quad \sigma_{x|y}^2 = \kappa \sigma_{y|x}^2. \quad (\text{H11})$$

The first term in Eq. (H3) is therefore

$$I(X_t; Y_t | x^{t-1}, y^{t-1}) = \frac{1}{2} \ln \left(1 + \frac{\varsigma_\tau^2}{\sigma_{y|x}^2} \right). \quad (\text{H12})$$

The second term is

$$\mathbb{E}[D(q_{t-1}^\tau \| p_t^\infty)] = \frac{1}{2} \left(\sigma_{x|y}^2 + \mathbb{E}[z_t^2] - \ln \sigma_{x|y}^2 - 1 \right), \quad (\text{H13})$$

with

$$z_t = (1 - \kappa) \mu_{t-1}^\tau + \kappa y_t - \ell_t. \quad (\text{H14})$$

The third term is

$$\mathbb{E}[D(p_{t-1}^\tau \| p_{t-1}^\infty)] = \frac{1}{2} \left(\varsigma_\tau^2 + \mathbb{E}[z_t'^2] - \ln \varsigma_\tau^2 - 1 \right), \quad (\text{H15})$$

with

$$z'_t = \mu_{t-1}^\tau - \ell_{t-1} = e^{-\tau}(x_{t-1} - \ell_{t-1}). \quad (\text{H16})$$

Given (x^{t-1}, y^{t-1}) , the only term depending on y_t is $\mathbb{E}[z_t^2]$ in Eq. (H13). It is optimized by choosing ℓ_t so as to have $z_t = 0$:

$$\hat{\ell}_t = \kappa y_t + (1 - \kappa)\mu_{t-1}^\tau = \kappa y_t + (1 - \kappa)[(1 - e^{-\tau})\ell_{t-1} + e^{-\tau}x_{t-1}]. \quad (\text{H17})$$

By taking $\ell_{t-1} = \hat{\ell}_{t-1}$, this defines recursively a series of optimal translations $\hat{\ell}^t$.

To express the optimal work, it remains to evaluate $\mathbb{E}[z_t'^2]$ for $\ell^t = \hat{\ell}^t$. Since $x_t - \hat{\ell}_t = (1 - \kappa)(x_t - \mu_{t-1}^\tau) - \kappa(y_t - x_t)$ where $x_t - \mu_{t-1}^\tau$ and $y_t - x_t$ are statistically independent, we have

$$\mathbb{E}[(x_t - \hat{\ell}_t)^2] = (1 - \kappa)^2 \varsigma_\tau^2 + \kappa^2 \sigma_{y|x}^2 = \sigma_{x|y}^2, \quad (\text{H18})$$

and therefore $\mathbb{E}[z_t'^2] = e^{-2\tau} \sigma_{x|y}^2$. All together, we obtain

$$\max_{\ell^t} \mathbb{E}[\mathcal{W}_t] = \frac{1}{2} \ln \left(1 + \frac{\varsigma_\tau^2}{\sigma_{y|x}^2} \right) - \frac{1}{2} \left(\sigma_{x|y}^2 - \ln \sigma_{x|y}^2 - 1 \right) + \frac{1}{2} \left(\varsigma_\tau^2 + e^{-2\tau} \sigma_{x|y}^2 - \ln \varsigma_\tau^2 - 1 \right), \quad (\text{H19})$$

which, given that $\varsigma_\tau^2 = 1 - e^{-2\tau}$ and $\sigma_{x|y}^2 = (\varsigma_\tau^{-2} + \sigma_{y|x}^{-2})^{-1}$, simplifies to $\max_{\ell^t} \mathbb{E}[\mathcal{W}_t] = \varsigma_\tau^2(1 - \sigma_{x|y}^2)/2$, or, in terms of τ and $\sigma_{y|x}^2$ only,

$$\max_{\ell^t} \mathbb{E}[\mathcal{W}_t] = \frac{1}{2} (1 - e^{-2\tau}) (1 - ((1 - e^{-2\tau})^{-1} + \sigma_{y|x}^{-2})^{-1}). \quad (\text{H20})$$

When $\tau \rightarrow \infty$, we recover the equilibrium result, $\mathbb{E}[\mathcal{W}_t] \leq I(X; Y) - \min_\phi \mathbb{E}_Y[D(P_{X|Y}(\cdot - Y) \| G_1(\cdot - \phi(Y)))]$, with $I(X; Y) = [\ln(1 + 1/\sigma_{y|x}^2)]/2$ and $\min_\phi \mathbb{E}_Y[D(P_{X|Y}(\cdot - Y) \| G_1(\cdot - \phi(Y)))] = D(G_{\sigma_{x|y}^2} \| G_1) = (\sigma_{x|y}^2 - \ln \sigma_{x|y}^2 - 1)/2$.